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***Ceraeochrysa lineaticornis* (Fitch, 1855)**

(Drawing by Marlin Peterson)

For details see: Ficitas, Penny, and Adams:
A Revision of the New World Genus Ceraeochrysa (*Neuroptera: Chrysopidae*)

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Sexual Dimorphism and Reproductive Biology in the Malagasy Snake Genus *Liopholidophis* (Lamprophiidae: Pseudoxyrhophiinae)

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The Malagasy snake genus *Liopholidophis* is unusual because reproductive modes vary among its six species and it presents extreme forms of body proportions and sexual dimorphism. This study confirms viviparity as the reproductive mode in *L. sexlineatus* on the basis of litters born in captivity (three other species are oviparous and reproductive mode is unknown in two species). Several sexually dimorphic characters involving body proportions exhibit greater magnitudes in *Liopholidophis* than are known in most other snakes. These include the extent of ontogenetic change in tail length between neonate and adult males of *L. sexlineatus*, relative tail lengths of males in five species, and the magnitude of sexual dimorphism in the number of tail vertebrae. Tails of adult males are extraordinarily long, averaging 71–118 % of snout-vent length in five species and 48% in *L. varius*. Tails of females are 33–55 % of snout-vent length. Tail length dimorphism (TLD) is present at birth in *L. sexlineatus*. Tail length in males shows strong positive allometry with respect to body size, whereas tail length in females is isometric or with slight positive allometry. Strongly male-biased sexual size dimorphism (SSD) occurs in all species except perhaps *L. dolicocercus* and *L. varius*, in which the mean sizes of adult males and females are similar. Male body sizes average 11–32 % greater than female sizes in *L. dimorphus, L. grandidieri, L. rhadinaea*, and *L. sexlineatus*.

For size and proportions, plesiomorphic characters within *Liopholidophis* are most likely absence of SSD or female-biased SSD, small TLD, and relatively short tails in males. *Liopholidophis varius* is probably the sister taxon to other species if these characters have evolved conservatively within this genus. Male-male mate competition and agonistic behavior and/or size advantages of males interacting with females during mating are probably the selective factors involved in the evolution of male-biased SSD and TLD in *Liopholidophis* but no direct observations support this supposition. In addition to *L. sexlineatus*, viviparity occurs in two species of *Stenophis* among Malagasy lamprophiids, whereas oviparity is characteristic of all others for which data exist. However, reproductive data for most species are unavailable or imprecise. Oviposition and births of Malagasy snakes are concentrated in the rainy season and early dry season, indicating strongly seasonal reproduction, as has been found in most other tropical snakes.

KEYWORDS: allometry, body size, Colubridae, life history, Lamprophiidae, *Liopholidophis*, Madagascar, natural history, neonates, Pseudoxyrhophiinae, reproduction, sexual dimorphism, snakes, viviparity

Reproductive modes, body size, and patterns of sexual dimorphism have important consequences for life history evolution and behavior, including feeding and reproductive ecology, mating systems, and thermoregulatory patterns (Krause et al. 2003; Shine 1993, 1994b; Vincent et al. 2004). For snakes, these aspects of life history have been best studied in temperate species of North America, Europe, and Australia but have been documented in detail for relatively few tropical snakes. Nonetheless, a full understanding of life history evolution in snakes requires a comprehensive understanding of tropical species, which sometimes differ in important respects from temperate taxa (Aldridge et al. 1995; Brown and Shine 2002; Fitch 1982). The ecological attributes and life histories of the snakes of Madagascar are among the most poorly documented of snake radiations on large tropical islands.

All but one of Madagascar's approximately 80 species of caenophidian snakes derive from a single colonizing lineage and the radiation displays ecomorphological diversity comparable in some ways to continental radiations with much higher species diversity (Cadle 2003; Kelly et al. 2008; Nagy et al. 2003). However, basic aspects of the natural history of Malagasy snakes, including modes of reproduction, clutch sizes, reproductive cycles, and patterns of sexual dimorphism have not been documented for most species. Nonetheless, both oviparous and viviparous modes of reproduction are known and novel patterns of sexual dimorphism occur in several genera (Cadle 2003).

This paper addresses several aspects of life history in the six species of the Malagasy snake genus *Liopholidophis* Mocquard, whose systematics was reviewed by Cadle (1996a, 1998), Cadle and Ineich (2008), and Glaw et al. (2007). These are diurnal, primarily terrestrial snakes that feed mainly on frogs or their eggs (Cadle 1996a). They are characterized in part by the especially elongate tails of males. Five of the six species inhabit closed-canopy rainforests, primarily at mid- to upper elevations in eastern Madagascar. A widespread species, *L. sexlineatus*, is semiaquatic and inhabits nonforested, wet habitats such as marshes, wet meadows, bogs, rice paddies, or stream edges (Cadle 1996a, 2003).

Two key aspects of life history are unusual in *Liopholidophis* (Cadle 1996a). First, modes of reproduction vary within the genus. Oviparity is known in *L. grandidieri* and *L. rhadinaea*, and probably occurs in *L. dolicocercus* (see later), whereas the presence of well-developed fetuses without accompanying mineralized shell membranes in dissected females has suggested that *L. sexlineatus* is viviparous (Cadle 1996a). The reproductive mode of *L. varius* and *L. dimorphus* is unknown. Second, patterns of sexual dimorphism in body size and tail length are unusual (Cadle 1996a; Glaw et al. 2007). Males attain larger snout-vent lengths than females. Male-biased size dimorphism is widespread among caenophidians but is less common than female-biased size dimorphism (Fitch 1981; Shine 1993). Furthermore, sexual dimorphism in tail lengths is among the most extreme documented for snakes, and in *L. grandidieri* and *L. sexlineatus* the tails of males commonly exceed the body in length, i.e., tails are longer than the snout-vent length. These are proportionally longer tails than are known in any other snakes. Although strong sexual dimorphism in tail lengths has been documented for all species of *Liopholidophis* (Cadle 1996a; Glaw et al. 2007), the relationship between tail length and body size has not been explored for any species.

Cadle (1996a:446) thought that exaggerated tail length dimorphism in *Liopholidophis* was probably present from birth but few small specimens were available to corroborate this supposition. In fact, the ontogeny of sexually dimorphic differences has been documented for only a few squamates and sexual dimorphism in snakes at birth has rarely been demonstrated (King 1997; King et al. 1999; Krause and Burghardt 2007; Shine 1993; Shine and Crews 1988). Nonetheless, understanding the proximate causes of sexually dimorphic differences (e.g., size differences at birth, differential growth rates and/or duration, differential survivorship, or timing of sexual matu-

rity) depends on a detailed examination of the relationship between sexual differences, body size, and allometric patterns (Badyaev 2002; Kaliontzopoulou et al. 2008; Shine 1990). Ideally, comparisons are made among individuals of known age (i.e., static and longitudinal allometry; Cock 1966) but this is rarely the case except in well-studied populations. Thus, most studies of sexual size dimorphism in reptiles compare dimensions of individuals of unknown age, with body size used as the reference for comparison (cross-sectional allometry). Cross-sectional allometric patterns can help understand the selective regimes ultimately responsible for the evolution of sexual dimorphism.

Documenting these aspects of life history will further our understanding of the behavior and evolution of *Liopholidophis* and contribute toward understanding life history evolution in Madagascar's snakes. In this paper I confirm viviparity as the reproductive mode in *L. sexlineatus* and present new data on clutch sizes, fecundity, and neonates. I document sexual dimorphism at birth and the relationship between size, tail length, and sexual dimorphism within *Liopholidophis*, and compare these patterns with other caenophidians. I evaluate the phylogeny of sexual dimorphism in body size and tail length in *Liopholidophis* and consider the selective forces influencing the evolution of male-biased size and tail length dimorphism. I review the reproductive biology of Malagasy snakes and urge more careful documentation of reproductive parameters in these snakes.

Material and Methods

Sampling and data collection.— Neonates of *Liopholidophis sexlineatus* were from two litters born to gravid females collected 21 January 2001 near the village of Ambatolahy, approximately 2.3 km NW of Ranomafana, 850 m elevation, Fianarantsoa Province, Madagascar (21.25°S, 47.43°E). The setting is a seasonal montane rainforest with annual rainfall varying from 1700 to 4300 mm and concentrated from December to March (Wright and Andriamihaja 2003). September and October are the driest months. Temperatures vary from 4–12°C (June to September) to 36–40°C (December to February). *Liopholidophis sexlineatus* is not routinely surface-active during the dry season but retreat sites and behavior patterns during this period are unknown.

On 1 February 2001 the snakes were transported to the Brookfield Zoo, Brookfield, Illinois, where they were maintained in the veterinary hospital for a 90-day quarantine period and where the births occurred. During transport and quarantine the snakes were given ad libitum access to water, fed frogs (reed frogs [*Heterixalus*] or tree frogs [*Hyla*]) twice per week, and treated for significant cestode and nematode infections. Data on the neonates were recorded 96 hours after birth (Litter 1) or 72 hours after birth (Litter 2). Neonates were not fed prior to data collection but were given ad libitum access to water. Subsequently, neonates were fed live Green Treefrog (*Hyla cinerea*) tadpoles placed in a water dish, frozen/thawed frogs, and pinky mice scented with frogs. A stillborn neonate in each clutch was not included in the morphological analyses and clutch mass calculations but they were counted as part of the clutch size.

Measurements of snout-vent lengths (SVL) and tail lengths (TailL), given in millimeters, were taken by stretching the body along a ruler. Masses of snakes collected and preserved in the field were determined using Pesola® scales to the nearest 0.1 g; obvious food items in the stomach were disgorged before weighing. Masses of captive neonates and adults were measured with an electronic balance to the nearest 0.01 g. Some of the data were summarized in a previous systematic study (Cadle 1996a) but data from additional specimens are included herein. I also used measurements of total lengths and SVLs for several species reported by Glaw et al. (2007), as follows: *L. sexlineatus* (eight males, seven females), *L. dimorphus* (one male, one female), *L. dolicocercus* (two males, one female), and *L. varius* (one female). Relative tail lengths were calculated as TailL/SVL,

a departure from the procedure in Cadle (1996a), in which relative tail length was calculated as TailL/Total Length. This departure facilitates comparisons to most studies of sexual dimorphism in snakes, which use the former index. Vertebral numbers for the trunk and tail were derived from ventral and subcaudal scale counts; sex disparities in the number of vertebrae were calculated as the female mean minus the male mean (Shine 2000). With the exception of *L. sexlineatus*, these species are uncommon to rare in collections and all are rare compared to species commonly studied in snake ecology. *Liopholidophis dimorphus* has been reported only from one male and one female (Glaw et al. 2007), whose measurements are included for comparative purposes but are not treated in the statistical analyses. The small samples reduced the power of some statistical tests.

Clutch sizes were determined from dissections of museum specimens and from captive births. Relative clutch mass (RCM) was calculated as neonate mass/female post-partum mass (Dunham et al. 1988:364–365; King 1989; Shine 1980). RCMs are conservative because a stillborn young from each clutch was not included. Cadle (1996a) staged embryos of *Liopholidophis* according to the system of Zehr (1962). These are here converted to the approximately equivalent stages of Dufaure and Hubert (1961) for comparison to other studies of squamate development (e.g., Andrews and Mathies 2000; Blackburn 1993).

Sexes of most specimens were determined by inspection of tail morphology, supplemented in some cases by examination of hemipenes or reproductive tracts (frequency distributions of relative tail lengths in males and females do not overlap in subadult and adult specimens; Cadle 1996a). For neonates, two discrete classes of relative tail length were apparent and a presumptive sex was assigned to each individual at birth based on its relative tail length. "Short-tailed" individuals were considered presumptive females and "long-tailed" individuals were considered presumptive males. Snakes that died during captivity (13 over five years) were dissected to confirm their sex. In all other cases, sexes were confirmed by their tail lengths during growth.

Size at first reproduction is not known for males or females of any species of *Liopholidophis*, although an approximate size at first reproduction of 333 mm SVL for female *L. sexlineatus* is estimated herein. For certain comparisons of "adult" morphology I assumed, for purposes of analysis, that adults were ≥ 333 mm SVL for either sex and for all species except *L. rhadinaea*, for which I assumed a minimum adult size of 250 mm SVL because of its overall small size (the smallest female *L. rhadinaea* with vitellogenic follicles in a previous study was 262 mm SVL; Cadle 1996a). These assumptions resulted in the exclusion of two males and six females from the "adult" sample of *L. sexlineatus*, one male from the "adult" sample of *L. dolicocercus*, and one male and two females from the "adult" sample of *L. rhadinaea*. All other specimens met the minimum criterion of adult size (juveniles are underrepresented in museum collections of these species). The assumption of identical sizes at sexual maturity in males and females is probably unrealistic but permitted maximal use of the available specimens in the absence of other data. For completeness all non-neonatal individuals, referred to as the "postnatal" sample, are included in the bivariate plots and frequency histograms, whether or not they were included in calculations of "adult" morphology; all individuals except neonatal *L. sexlineatus* were included in the general regression analyses.

Statistical methods.— Differences between frequency distributions of relative tail lengths were tested for significance by the Mann-Whitney *U*-test in pairwise comparisons. In cases involving adult samples with $n > 20$, I used a modified *t*-test with the test statistic, t_s, calculated by procedures in Sokal and Rohlf (1981:432–437). The significance of differences between mean SVLs or tail lengths in paired comparisons (e.g., between litters or between sexes within species) was tested using *t*-tests after first testing for normality and homogeneity of variances.

Relationships between SVL and clutch size, tail length, and mass were assessed using least-

squares regression and correlation for each sex separately within species. All variables were transformed to logarithms (base 10) for analysis. Significance of regressions was tested by analysis of variance and regression slopes were tested for homogeneity by appropriate *F*-tests. For comparisons among species I used single-classification analysis of covariance (ANCOVA) with species as the factor, TailL as the dependent variable, and SVL as the covariate. Unplanned multiple comparisons tests (Sokal and Rohlf 1981:525–526) were subsequently used to compare adjusted among-species means. Least-squares (Model I) regression tends to underestimate regression slopes in cases where both variables are estimated with error. Consequently, some authors recommend the use of Model II regression techniques for analyzing allometric relationships (Fairbairn 1997, 2007; LaBarbera 1989). However, least-squares regression is appropriate when prediction of the dependent variable is the primary goal (Sokal and Rohlf 1981), which is the case in most studies of the allometry of body proportions in snakes. The results of Model I and Model II regressions are expected to be similar when the error rates of both variables are of similar magnitude and correlation coefficients are high (McArdle 1988). Both conditions apply to data analyzed herein.

It was not possible to obtain a regression of tail length on SVL for females of *Liopholidophis grandidieri* because only three females are known. To calculate indices of sexual dimorphism in tail length for this species, I estimated the regression line for females as follows. Regression slopes for the relationship between tail length and SVL for females of all species of *Liopholidophis* (except *L. grandidieri*) are very similar, but the relative tail length of female *L. grandidieri* is much greater than that of females of the other species (RESULTS, Table 1). Thus, I calculated the regression for the pooled sample of females of all species combined, excluding *L. grandidieri*, and used the resulting regression slope as the estimated slope for *L. grandidieri*. I then used the point defined by the means of the tail lengths and SVLs (log transformed) of the three female *L. grandidieri* and calculated a regression line through this point using the slope from the pooled female regression. This estimated regression was used in calculating the index of sexual dimorphism for tail length in *L. grandidieri*.

I used relative tail lengths (RTLs) as an adjunct to the regression analyses in testing the significance of their correlation with SVL for comparisons between males and females within species. Proportional data such as RTLs have some undesirable properties for most statistical analyses but can be used to inform certain types of biological relationships. In these cases, arcsine transformation is generally recommended but is usually not necessary when the proportions are between 30% and 70% (Sokal and Rohlf 1981). Mean RTLs for three species were outside this range, and these are the only three for which arcsine transformation affected the calculated means of RTL: for *L. dolicocercus* males, 0.78 versus 0.79; for *L. grandidieri* males, 1.18 versus 1.16; and for *L. sexlineatus* males, 0.90 versus 0.93 (untransformed RTL versus transformed RTL, respectively); standard errors of the means were smaller in all cases using the transformed variables and the significance levels for all correlation coefficients were unaffected by transformation. Thus, I present comparisons of RTL using the untransformed variables so that they are directly comparable to those in the literature.

Measures of sexual dimorphism.— I used several indices of sexual dimorphism (ISD) for comparative purposes (for reviews see Fairbairn 2007 and Lovich and Gibbons 1992). I evaluated sexual dimorphism in body size (SVL) with two measures: (1) Lovich and Gibbons (1992) ISD = mean adult SVL of the larger sex divided by the mean adult SVL of the smaller sex (back-transformed from logarithms), with the resulting quotient subtracted from 1.0. The result was arbitrarily expressed as negative if males were the larger sex and positive if females were the larger sex. (2) King et al. (1999) ISD = mean SVL of males/mean SVL of females, calculated for neonate and adult size classes. For these measures, a greater degree of sexual dimorphism is reflected by

increasing absolute values of each index. To quantify sexual dimorphism in tail length I used Shine's (1991) method: using log-transformed variables, I obtained regression equations relating female tail length to SVL and used these to calculate the expected tail length of a female with a SVL equal to the mean male SVL. These "adjusted female tail lengths" were then divided by "adjusted male tail lengths" (both back-transformed from logarithms) calculated in a similar way, resulting in a measure of sexual dimorphism adjusted to mean male size. For this measure, a greater degree of sexual dimorphism is reflected by smaller values of the index.

Taxonomic conventions.— Names of snake lineages used in this paper follow Zaher et al. (2009), who divided the traditional Colubridae *sensu lato* into a number of families because of its paraphyly with respect to viperids and elapids. All Malagasy caenophidians except *Mimophis* belong to the lineage Pseudoxyrhophiinae of the family Lamprophiidae; *Mimophis* is in the family Psammophiidae. Other familiar groups are also treated as families, e.g., Natricidae (formerly Natricinae), Colubridae (formerly Colubrinae), Homalopsidae (homalopsines), and Dipsadidae (Neotropical xenodontines *sensu lato*). In a few cases when referencing older studies that used "Colubridae" in its traditional sense, I use the name "colubrid" in quotes explicitly to refer to the traditional (but paraphyletic) taxon used in the older studies (i.e., all caenophidians excluding *Acrochordus*, viperids, and elapids).

RESULTS

Reproductive Parameters for *Liopholidophis sexlineatus*

Three of six females of *Liopholidophis sexlineatus* collected 21 January 2001 were pregnant. These gave birth to 10 young on 7 March 2001, 12 young on 30 March 2001, and 5 young on 4 April 2001. The last litter was only a partial delivery and was followed on 11 April by a stillborn fetus and death of the female shortly thereafter. Further consideration of these litters focuses on the litters born 7 and 30 March. Young emerged from their embryonic membranes as they were being born or within a few minutes. These captive births confirm viviparity in *L. sexlineatus*, which had been inferred previously on the basis of the presence of fetuses in dissected museum specimens (Cadle 1996a).

Clutch sizes in *Liopholidophis sexlineatus* range from 4–12 (mean clutch size, 7.9) and the correlation between female SVL and clutch size is significant (Fig. 1; $r = 0.71$, $P = 0.02$). The smallest pregnant female was 333 mm SVL, which establishes an estimate of the minimum size at sexual maturity for females; this individual also had one of two smallest clutch sizes, four young (Fig. 1). The total mass of the two litters and corresponding masses of the dams were 23.08 g (dam mass, 59.95 g) and 17.59 g (dam mass, 46.7 g), resulting in relative clutch masses (RCM) of 0.385 and 0.376, respectively. Of the three non-gravid females collected 21 January 2001, two were probably not sexually mature based on their sizes (SVLs < 300 mm, masses 17.5–23.7 g). The third female (49.3 g) mated in captivity and gave birth to three stillborn young and five large yolk masses without signs of developing fetuses on 25 January 2002.

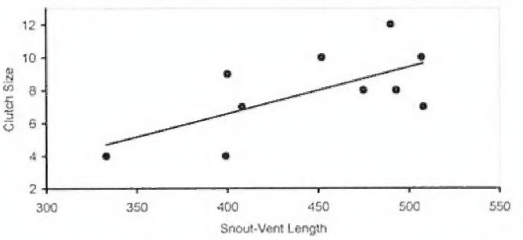


FIGURE 1. Relationship between female body size (SVL) and clutch size in *Liopholidophis sexlineatus*.

Museum specimens and field collections indicate that females of *Liopholidophis sexlineatus* are gravid during the rainy season in southeastern Madagascar (December to March). For the Ambatolahy population, five of nine females collected 8 December 1990 (Cadle 1996a) and three

of six females collected 21 January 2003 were pregnant. At another locality in southern Madagascar, Kalambatritra (23.41°S, 46.46°E), two females collected 23 December 2001 were carrying four and seven fetuses. Fetuses from females collected 8 December 1990 were in Dufaure and Hubert (1961) stages 30–31 (Cadle 1996a), or about one-quarter of the way through development as measured by embryo size (Andrews and Mathies 2000). Thus, embryogenesis apparently begins just prior to, or coincident with, the onset of the rainy season. Young are born during the rainy season or as rainfall begins tapering off in March or April.

Neonates and Tail Length Dimorphism in *Liopholidophis sexlineatus*

Table 1 reports descriptive statistics on size, body proportions, and mass of *Liopholidophis sexlineatus*; frequency distributions of relative tail lengths (RTLs) of neonates and postnatal individuals are shown in Fig. 2. The frequency distributions of RTLs in postnatal males and females differ significantly (Mann-Whitney *U*-test, $U_{s\,[23,\,25]} = 598$, $t_s = 6.41$, df = ∞, $P << 0.0001$; Fig. 2). Considering only individuals in the adult size class, mean tail lengths of adult males are greater than those of adult females ($t = 9.59$, df = 21, $P << 0.0001$). The average tail length of adult males is 90% of SVL, whereas tail lengths in females average only 39% of SVL.

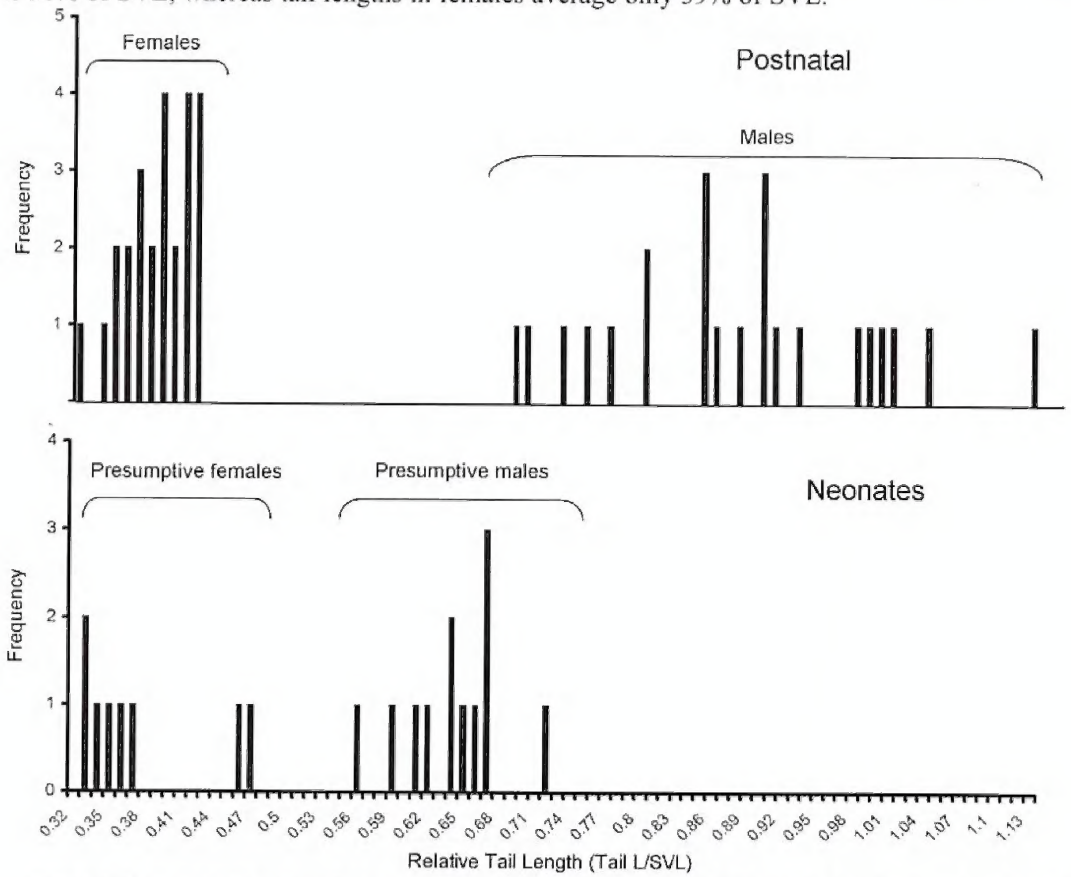


FIGURE 2. Frequency histograms of relative tail lengths in *Liopholidophis sexlineatus*. The postnatal sample includes all individuals that were not part of the captive-born litters examined. The neonatal sample comprises the two litters described herein with the presumptive sex of each individual indicated, based on its relative tail length at birth (see *Material and Methods*).

TABLE 1. Descriptive statistics on body measurements and mass for species of *Liopholidophis*. The top portion of the table presents data for neonates from two litters of *L. sexlineatus* separately and combined. Then follow data for adult samples of all species (as defined in Material and Methods). Values are mean ± S. E. followed by range (for combined litters and adult samples). Sample sizes in parentheses follow each sex. P-values below the male SVL and Tail Length statistics are one-tailed probabilities that the male mean > female mean for each intraspecific comparison.

Species	Sex	SVL (mm)	Tail length (mm)	Relative tail length	Mass (g)
L. sexlineatus (neonates)					
Litter 1	Males (7)	136.8 ± 1.32	84.7 ± 1.78	0.62 ± 0.014	1.94 ± 0.05
	Females (2)	135.0 ± 4.00	45.5 ± 0.50	0.34 ± 0.006	1.99 ± 0.05
Litter 2	Males (5)	129.8 ± 4.78	87.0 ± 2.39	0.67 ± 0.014	2.07 ± 0.10
	Females (6)	132.7 ± 1.93	51.8 ± 3.71	0.39 ± 0.024	2.12 ± 0.08
Combined litters	Males (12)	133.9 ± 2.26	85.7 ± 1.41	0.64 ± 0.012	1.99 ± 0.05
		112–142	75–93	0.56–0.72	1.74–2.30
		$P = 0.44$	$P < 0.0001$	$P < 0.0001$	$P = 0.23$
	Females (8)	133.3 ± 1.64	50.3 ± 2.91	0.38 ± 0.024	2.09 ± 0.06
		124–139	41–63	0.33–0.47	1.75–2.29
L. sexlineatus (adults)	Males (21)	477.2 ± 20.29	434.3 ± 27.78	0.90 ± 0.023	47.6 ± 8.92 (6)
		336–675	243–735	0.69–1.13	22.0–73.0
		$P = 0.02$	$P < 0.0001$	$P < 0.0001$	
	Females (19)	429.7 ± 10.53*	164.3 ± 4.46	0.39 ± 0.006	Non-pregnant: 54.8 ± 4.87 (4)
		333–508	130–196	0.34–0.42	46.6 – 66.0
					Pregnant: 61.3 ± 7.49 (7)
					30.3 – 85.0
L. dimorphus†	Male (1)	615	457	0.74	
	Female (1)	536	224	0.42	
L. dolicocercus	Males (6)	593.1 ± 49.57	471.0 ± 61.95	0.78 ± 0.043	
		514–770	328–698	0.64–0.96	
		$P = 0.43$	$P = 0.007$	$P = 0.0002$	
	Females (5)	605.6 ± 38.22	250.4 ± 15.67	0.41 ± 0.006	
		494–705	200–287	0.40–0.43	
L. grandidieri	Males (4)	549.5 ± 63.33	654.3 ± 94.22	1.18 ± 0.052	
		442–732	461–904	1.04–1.28	
		$P = 0.06$	$P = 0.01$	$P = 0.0001$	
	Females (3)	416.7 ± 10.09	230.0 ± 10.60	0.55 ± 0.026	
		402–436	209–243	0.51–0.60	
L. rhadinaea	Males (5)	371.2 ± 25.83	263.0 ± 22.86	0.71 ± 0.020	
		281–429	198–320	0.65–0.75	
		$P = 0.02$	$P = 0.001$	$P < 0.0001$	
	Females (9)	291.8 ± 6.37	103.8 ± 2.82	0.36 ± 0.008	
		262–313	84–115	0.32–0.40	
L. varius	Males (6)	487.0 ± 24.57	235.7 ± 16.92	0.48 ± 0.013	
		422–590	185–300	0.43–0.51	
		$P = 0.34$	$P = 0.003$	$P < 0.0001$	
	Females (4)	471.9 ± 25.35‡	149.5 ± 12.55	0.33 ± 0.005	
		359–578	115–175	0.32–0.34	

* Sample size for female SVL for *L. sexlineatus* was 21 (two females with incomplete tails were not included in the other statistics).
† *L. dimorphus* has been reported from only one male and one female (Glaw et al. 2007). ‡ Sample size for female SVL for *L. varius* was seven (three females with incomplete tails were not included in the other statistics).

The tails were equal to, or exceeded, the body in length (RTLs ≥ 1) in four of 23 postnatal males, but these individuals spanned SVLs of 384 – 650 mm, essentially throughout the size range of adult males. The five postnatal males with the shortest RTLs (≤ 0.80, Fig. 2) were also five of six individuals with the shortest SVLs (259–372 mm); two individuals with RTL = 0.80 had SVLs of 347 mm and 495 mm. These patterns suggest that in postnatal males, short-tailed individuals tend to have small body sizes (short SVL) but that long-tailed males may be either small or large in body size (this pattern is reflected in data for male *L. dolicocercus*, *L. grandidieri*, and *L. rhadinaea* as well, even with the small samples available).

Among neonates, two size classes of relative tail length are apparent. One class ("short-tailed"; RTLs 0.33–0.47) comprised presumptive females and the other ("long-tailed"; RTLs 0.56–0.72) comprised presumptive males; these have significantly different distributions (Fig. 2; Mann-Whitney *U*-test, $U_{s\,[12,\,8]} = 96$, $P < 0.001$). Means of SVL, TailL, and mass were not significantly different between litters for presumptive males or presumptive females considered separately; subsequent analyses used pooled samples of each sex. For the pooled samples, males and females do not differ in mean SVL or mass (Table 1). In contrast, the mean tail length of presumptive males (85.7 mm) compared to the mean of presumptive females (50.3 mm) was highly significant ($t = 12.12$, df = 18, $P < 0.0001$).

Dissections of neonates that died confirmed the presumptive sexes assigned at birth. Two neonatal females had much longer tails than any other female (RTLs 0.46, 0.47; Fig. 2) and I questioned their presumptive sex. These individuals were transferred to other institutions at 1.9 and 5.1 years of age; external inspection before transfer was consistent with their assignment as females. Thus, strong sexual dimorphism in tail length is present at birth in *Liopholidophis sexlineatus*. However, the frequency distributions of relative tail lengths of neonatal males and females are less distinct than in adults (Fig. 2). In females the mean relative tail length does not differ between the neonate and adult classes (0.38 vs. 0.39; $t_s = 1.38$, df = ∞, NS). In contrast, the difference between mean relative tail lengths of male neonates and adults is highly significant (0.64 vs. 0.90; $t_s = 4.73$, df = ∞, $P < 0.0001$). In other words, compared to females, the tails grow relatively longer in males between the neonate and adult classes.

These patterns are reflected in the relationship between body size and tail length, which shows that males always have longer tails than females of a given size and that the difference between male and female tail lengths increases with size (Fig. 3) (excluding neonates, heterogeneity of slopes test with sex as the factor and SVL as the covariate, $F = 336.5$, df = 1, 44; $P < 0.0001$). The slope of the relationship between TailL and SVL for females is not significantly different from 1.0 ($t_s = 1.8$, df = 23, $P = 0.087$), indicating isometry between tail length and body size. On the other hand, the slope of the same relationship for males is highly significant ($t_s = 6.14$, df = 21, $P < 0.001$), indicating strong positive allometry of tail length with respect to body size in males.

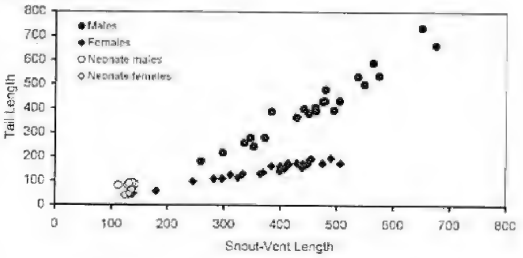


FIGURE 3. Relationship between tail length and body size in *Liopholidophis sexlineatus*. Solid symbols include all postnatal individuals. For ease of interpretation the raw data are plotted but in all analyses the data were log-transformed. See Fig. 5 for regressions of log-transformed data.

Thus, virtually all of the increase in tail length dimorphism with increasing size is due to the positive allometry of the tail relative to SVL in males. The mean relative tail lengths in neonate and adult females are almost the same (Table 1) and the correlation of RTL with SVL is not significantly different from zero ($r = 0.32$, $t = 1.61$, df = 23, NS) (Fig. 4). In contrast, RTL in males increas-

es with increasing SVL, with no clear asymptote at the largest sizes (Fig. 4). The correlation between RTL and SVL in males is highly significant ($r = 0.80$, $t = 6.15$, df = 21, $P < 0.001$). Size-adjusted measures of tail length dimorphism in *Liopholidophis sexlineatus* are considered below in comparison to other species of the genus.

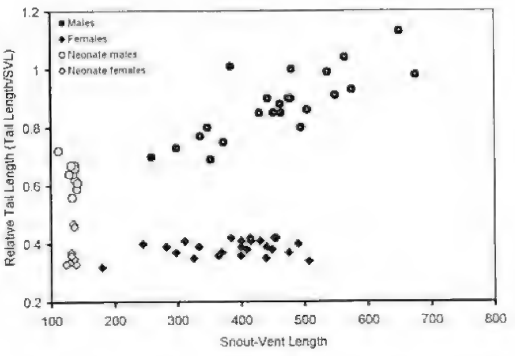


FIGURE 4. Relationship between relative tail length and body size in *Liopholidophis sexlineatus*. Solid symbols include all postnatal individuals.

The relative variability of tail length in males and females differs between neonates and adults, as suggested by the frequency distributions (Fig. 1). Coefficients of variation (V) of tail length for male and female neonates are significantly different, with females the more variable sample ($V = 0.013$ and 0.040 for males and females, respectively; $F_s = 7.156$, $P < 0.01$). This difference is due to the two females with unusually long tails (Fig. 1); excluding these individuals, the relative variability of tail lengths of neonate males and females is not significantly different. For the adult samples, males are more variable than females ($V = 0.048$ and 0.024 for males and females, respectively; $F_s = 5.78$, $P < 0.001$).

Interspecific Comparisons of Tail Lengths

The relationships between body size and tail length in other species of *Liopholidophis* are similar to the patterns shown by *L. sexlineatus* but differ in details (Table 1; Fig. 5). Mean relative tail lengths in males ranged from 0.48 (*L. varius*) to 1.18 (*L. grandidieri*), and for females from 0.33 (*L. varius*) to 0.55 (*L. grandidieri*), with *L. rhadinaea*, *L. dolicocercus*, and *L. sexlineatus* in the same relative order between these extremes for both sexes. All four males of *L. grandidieri* had tails exceeding the body in length (RTLs 1.04 – 1.28). Thus, *L. sexlineatus* and *L. grandidieri* are exceptional in that the tails of adult males can sometimes exceed the body length. Tails of females are less than half the body length (RTLs 0.33 – 0.41) in all species except *L. grandidieri* (RTLs 0.51–0.60).

Regressions of TailL on SVL were significant for each sex with the exception of female *Liopholidophis grandidieri*, which was nonsignificant because the three specimens were very similar in SVL (Table 2, Fig. 5); regression parameters for female *L. grandidieri* were estimated as explained in MATERIAL AND METHODS. Tests for heterogeneity of slopes between males and females within species were all highly significant ($P \leq 0.001$ for all pairwise comparisons). Analyses of covariance of the relationship between tail lengths and body size showed that among-species slopes for neither males nor females differ significantly. Tail length differences overall are highly significant among species in separate analyses for each sex (Table 3). For males, multiple comparisons

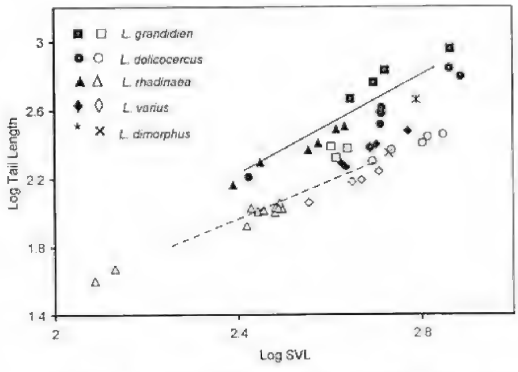


FIGURE 5. Interspecific comparisons of the relationship between tail length and body size for *Liopholidophis*. Closed symbols are males; open symbols are females. Axes are in common logarithms. Solid and dashed lines are regression lines for male and female *L. sexlineatus*, respectively, for reference; individual points for this species are not plotted (see Fig. 3).

TABLE 2. Comparisons of linear regressions of Log Tail Length on Log SVL for species of *Liopholidophis*. Significance of the slopes for each regression, as well as for the difference between slopes for males and females within species are indicated. Range for slopes and intercepts represent 95% confidence limits. *r*, correlation coefficient. SE, standard error of the correlation coefficient.

Species	Males			Females			
	Intercept	Slope	*r* SE	Intercept	Slope	*r* SE	Slope difference between males and females
L. sexlineatus	−1.212	1.435	0.98	− 0.690	1.107	0.97	$F_S = 336.52$ [1, 44]
	−1.60 – −0.82	1.29 – 1.58	0.03	−1.02 – −0.36	0.98 – 1.23	0.03	$P < 0.001$
		$P < 0.0001$			$P < 0.0001$		
L. dolicocercus	− 1.078	1.351	0.98	-0.338	0.983	0.98	$F_S = 757.30$ [1, 8]
	−1.89 – −0.26	1.05 – 1.65	0.04	−1.39 – 0.71	0.60 – 1.36	0.01	$P < 0.001$
		$P < 0.0001$			$P = 0.004$		
L. grandidieri	− 0.673	1.272	0.97	NS	NS	0.1	____
	−3.35 – 2.00	0.29 – 2.25	0.04	(− 0.578)*	(1.122)	0.05	
		$P = 0.03$					
L. rhadinaea	-0.92	1.298	0.98	-0.591	1.057	0.99	$F_S = 635.18$ [1, 13]
	−1.81 – −0.03	0.95 – 1.65	0.03	−0.92 – −0.27	0.92 – 1.19	0.03	$P < 0.001$
		$P = 0.0005$			$P < 0.0001$		
L. varius	− 1.458	1.425	0.97	− 0.980	1.191	0.99	$F_S = 769.35$ [1, 6]
	− 2.69 – −0.22	0.97–1.88	0.02	−1.64 – −0.32	0.94–1.44	0.01	$P < 0.001$
		$P = 0.001$			$P = 0.002$		
Liopholidophis All species	−1.03	1.35	0.83	−0.784	1.14	0.96	$F_S = 553.01$ [1, 92]
	−1.75 – −0.31	1.08 – 1.62	0.12	−1.04 – −0.53	1.04 – 1.24	0.05	$P < 0.001$
		$P < 0.0001$			$P < 0.0001$		

* The regression for female *L. grandidieri* was not significant. Estimated regression slope and intercept were calculated as described (Material and Methods).

tests show that mean tail lengths of *L. grandidieri*, *L. sexlineatus*, and *L. varius* are significantly different from one another, and from *L. dolicocercus* and *L. rhadinaea*, after accounting for SVL ($P < 0.01$ for all comparisons); mean tail lengths of male *L. dolicocercus* and *L. rhadinaea* are not significantly different ($P > 0.05$). For females, multiple comparisons tests of *L. varius* compared to *L. dolicocercus* and *L. sexlineatus*, but no other comparisons, were significant ($P < 0.01$) (*L. grandidieri* was not included in the ANCOVA for females because no significant regression was obtained).

Slopes of the relationship between TailL and SVL suggest different allometric patterns between males and females, although slopes for both sexes of all species are positive. As shown above for *Liopholidophis sexlineatus*, tail length in males is positively allometric with respect to

TABLE 3. Results of analysis of covariance testing for differences among species of the relationship between tail length (dependent variable) and body size (SVL as the covariate).

Source of variation	df	SS	MS	*F*s
		Males		
Species	4	0.452792	0.113198	101.939 ***
Error	40	0.044418	0.00111045	
		Females		
Species	3	0.018205	0.0060684	7.756 ***
Error	39	0.0305158	0.00078246	

***, $P < 0.001$.

body size, whereas tail length in females is suggestive of isometry but is marginally non-significant. These sexual differences are reflected in the other species, which have many fewer degrees of freedom (2–9) for statistical analysis. Slopes for females of each species considered separately, and for males of *L. grandidieri* and *L. rhadinaea*, were not significantly different from 1.0 (that for male *L. rhadinaea* was only marginally non-significant). Regression slopes for male *L. dolicocercus* and *L. varius* were significantly greater than 1.0 ($P < 0.05$). However, combined analyses of all males (all species) and for all females (all species) resulted in a positive regression coefficients significantly different from 1.0 (males: coefficient = 1.35, $t_s = 2.69$, df = 45, $P < 0.01$; females: coefficient = 1.14, $t_s = 2.8$, df = 47, $P < 0.01$). These patterns suggest that tail lengths in females are isometric or slightly positively allometric with respect to body size, whereas for males this relationship shows strong positive allometry.

These allometric relationships are reflected by the correlations between relative tail lengths and body size. As in *Liopholidophis sexlineatus*, RTLs in females of all species of *Liopholidophis* show no significant correlation with SVL. For males, positive correlations between RTL and SVL for *L. dolicocercus* ($r = 0.81$, $t = 3.050$) and *L. varius* ($r = 0.82$, $t = 2.889$) were significant ($P < 0.05$ in each case); the correlations were nonsignificant for male *L. grandidieri* ($r = 0.64$, $t = 1.170$, $P = 0.36$) and *L. rhadinaea* ($r = 0.77$, $t = 2.446$, $P = 0.07$) because of small sample sizes. For the combined sample of all males of all species, the correlation between RTL and SVL was highly significant ($r = 0.66$, $t = 5.405$, $P << 0.001$); for all females combined the correlation was nonsignificant ($r = 0.03$, $t = 0.204$, $P = 0.84$). Thus, in all species of *Liopholidophis* RTLs change little or not at all with increases in body size in females, whereas there is a strong positive relationship between RTL and body size in males.

In some respects the two species at the extremes of the distribution of relative tail lengths, *Liopholidophis varius* (low) and *L. grandidieri* (high), are outliers compared to other species in interspecific comparisons by sex. For example, in Fig. 5 the points for male *L. varius* and female *L. grandidieri* deviate below and above, respectively, the point clusters for the respective sexes of the other species. *Liopholidophis varius* not only has the shortest mean RTLs for each sex, the male mean (0.48) is much less than any other species (means 0.71–1.18) (Table 1). Furthermore, individual scores of RTL for male *L. varius* (0.43–0.51) do not overlap those of any other species (combined ranges 0.64–1.28); the ranges for individual values of RTL overlap for all other species except *L. grandidieri*, in which the individual values of males overlap only those of *L. sexlineatus* (Table 1). The contrasting situation applies to RTLs of female *L. grandidieri* in comparison to all other females (Table 1, Fig. 5). Thus, tails of male *L. varius* are shorter than expected compared to

males of the other species, and vice versa for female *L. grandidieri* compared to other females of similar body size.

These conclusions are supported by standardized residuals for male *Liopholidophis varius* and female *L. grandidieri* in the common regression of TailL on SVL for all males and all females, respectively. For male *L. varius* standardized residuals (−1.97 – −2.47) are greater in magnitude than any other values (the closest approaches in absolute value, but opposite direction, are standardized residuals for male *L. grandidieri*: 1.13 – 1.85) and only two other males had standardized residuals > 1 (1.07 and 1.36 for *L. sexlineatus*). Standardized residuals for female *L. grandidieri* (2.23 – 3.75) are at least an order of magnitude greater than those for nearly all other females; only six other females had standardized residuals > 1 in absolute value: four *L. varius* (−1.25 – −1.52) and one individual each of *L. rhadinaea* (−1.12) and *L. sexlineatus* (−1.35). The standardized residuals indicate that tail lengths of male and female *L. grandidieri* are high in relation to individuals of the other species with similar SVLs and sex, and, conversely, that tail lengths of male and female *L. varius* are both low compared to individuals of the other species with similar SVLs and sex. The magnitude of these deviations is greater for male *L. varius* (compared to conspecific females) and greater for female *L. grandidieri* (compared to conspecific males).

Sexual Dimorphism in Tail Length, Body Size, and Mass

Size-adjusted measures of sexual dimorphism in tail length (Table 4) quantify patterns suggested by the regressions of TailL on SVL (Figs. 3, 5). As a group, *Liopholidophis dolicocercus*, *L. grandidieri*, *L. rhadinaea*, and *L. sexlineatus* have similar indices (0.44 – 0.55) and are more strongly dimorphic in tail length than *L. varius* (0.71). Tail length dimorphism of neonatal *L. sexlineatus* (0.59) is intermediate between these two groups.

Mean SVLs range from 371 – 593 mm in males and 292 – 606 mm in females (Table 1). Body sizes reflect the pattern of male-biased size dimorphism for most species inferred in previous analyses (Cadle 1996a). The largest specimens in all species are males, but in *Liopholidophis dolic-*

TABLE 4. Measures of tail length dimorphism (TLD) and sexual size dimorphism (SSD; Lovich and Gibbons 1992; King et al. 1999) in *Liopholidophis*. Adjusted male and female tail lengths (Adj. ♂ TailL, Adj. ♀ TailL) (Shine 1991) corresponding to each measure of TLD are given.

Species	TLD (Adj. ♂ TailL, Adj. ♀ TailL)	SSD (Lovich–Gibbons)	SSD (King et al.)
L. dolicocercus	0.55 (452.9, 240.4)	+ 0.033	0.98
L. grandidieri	0.48 (633.9, 306.9)	– 0.297	1.32
L. rhadinaea	0.51 (257.0, 131.8)	– 0.262	1.27
L. sexlineatus Adults	0.44 (425.4, 187.8)	– 0.097	1.11
L. sexlineatus Neonates	0.59*	– 0.005	1
L. varius	0.71 (231.7, 165.2)	– 0.031	1.03

* Neonatal *L. sexlineatus* are not sexually dimorphic in SVL (Results) and the regression equation of tail length on SVL for adults may not apply to neonates. Thus, the index of TLD was calculated using the mean neonatal tail lengths, rather than the size-adjusted tail lengths as in the other calculations.

ocercus and *L. varius* the mean adult SVLs of males and females are almost the same (mean male SVLs 98% and 103% that of females, respectively). For the other four species, male SVLs average 11 – 32% greater than mean female SVLs. Mean adult SVLs for males and females are not significantly different for *L. dolicocercus, L. grandidieri,* and *L. varius* (Table 1). The marginal non-significance for *L. grandidieri* is due to small samples of both males and females and the large variance of male SVLs. On the other hand, the case for size dimorphism in *L. dolicocercus* and *L. varius* is equivocal. In addition to nearly equivalent mean SVLs for each sex, the largest males in these species differ minimally from the largest females (*L. dolicocercus*: 65 mm; *L. varius*: 12 mm) (Table 1). A caveat to these inferences is that precise estimates of size at first reproduction (particularly in males) are lacking for most species, which could affect estimates of mean adult size.

Indices of sexual size dimorphism (SSD) in *Liopholidophis* range from −0.297 – +0.033 (Lovich–Gibbons measure) or 0.98 – 1.32 (King et al. measure) (Table 4). *Liopholidophis grandidieri* and *L. rhadinaea* exhibit the greatest degree of SSD by either measure, followed by *L. sexlineatus* adults. *Liopholidophis dolicocercus*, *L. varius*, and neonatal *L. sexlineatus* are minimally sexually dimorphic in body size. Interestingly, the species with the greatest SSD, *L. grandidieri* and *L. rhadinaea*, are at opposite extremes of the size range of the species (large and small, respectively). The three species with the greatest body size dimorphism indices (*L. grandidieri, L. rhadinaea*, and *L. sexlineatus* adults) also have the greatest indices of tail length dimorphism (Table 4) but the overall correlation between the indices of size dimorphism and tail length dimorphism is non-significant ($r = 0.55$, $P > 0.05$).

Few data on body mass are available for analysis of sexual differences in body mass for species of *Liopholidophis*, especially when the confounding effects of pregnant females are eliminated. In *L. sexlineatus* regression slopes of body mass on SVL are significantly different between males and females ($F = 95.67$, df = 1, 10; $P < 0.001$; pregnant females excluded) (Fig. 6). The regressions suggest that in *L. sexlineatus* females have greater body mass at smaller SVLs (< 400 mm SVL), whereas at larger SVLs males have greater masses, perhaps in part due to the unusual length of the tails in larger males.

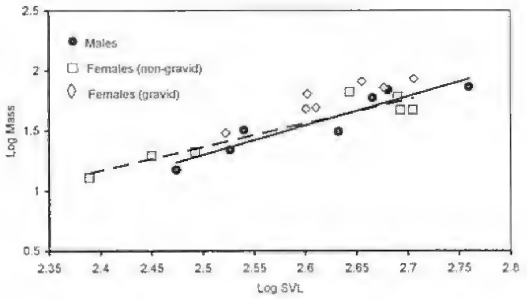


FIGURE 6. Relationship between mass and body size (SVL) in *Liopholidophis sexlineatus*. Axes are in common logarithms. Solid and dashed lines are regressions for males and non-gravid females, respectively. Gravid females are plotted but not included in the calculated regression.

This pattern may characterize other species of *Liopholidophis*, in which males and females generally have comparable body shapes. However, in *L. dolicocercus*, in which strong sexual dimorphism in SVL remains to be demonstrated, large females attain relatively massive body and head proportions, whereas males have a slender body shape similar to other species of *Liopholidophis* (Cadle, unpublished data). Few data on mass are available for *L. dolicocercus*, but a comparison of two specimens with similar total length illustrates the dramatic differences in body shape (as reflected by mass). A female (Museum of Comparative Zoology 180409; 652 mm SVL, 277 mm TailL, 929 mm total length) had a mass of 89 g; a male of nearly identical total length (MCZ 180405; 517 mm SVL, 411 mm TailL, 928 mm total length) had a mass of only 48 g. Along with the similar adult SVLs attained by male and female *L. dolicocercus* (Table 1), this suggests that patterns of size dimorphism in this species may be different from other species of *Liopholidophis*. Further resolution will require more specimens of this uncommon species.

Sex Differences in Vertebral Numbers

As might be expected from the relative proportions of body and tail, males have more trunk vertebrae and considerably more tail vertebrae than females (Table 5). *Liopholidophis varius*, the species with the least dimorphism, also has the least sex disparity in trunk and tail vertebrae, whereas the disparities in the other species are greater. Among the remaining five species, sex disparities do not closely correlate with the magnitudes of dimorphism in body size or tail length. Overall, there is also no significant correlation between sex disparity in tail vertebrae and sex disparity in trunk vertebrae. The failure to demonstrate these correlations is likely due to the small sample sizes and the small range and wide scatter of the data, particularly for disparity in trunk vertebrae.

TABLE 5. Vertebral numbers in *Liopholidophis*. For each species the mean numbers of trunk and tail vertebrae for males and females, respectively, are given, followed by the disparity in vertebral count between males and females (female mean minus the male mean). Sample sizes are given in Table 1.

Species	Trunk vertebrae	Tail vertebrae
L. dimorphus	163, 146	134, 79
	−17	−55
L. dolicocercus	156, 145	154, 84
	−11	−70
L. grandidieri	166, 155	216, 111
	−11	−105
L. rhadinaea	175, 156	131, 74
	−19	−60
L. sexlineatus	153, 143	150, 74
	−10	−76
L. varius	151, 144	94, 69
	−7	−25

Liopholidophis grandidieri and *L. rhadinaea*, the two species with the greatest sexual size dimorphism (Table 4), also exhibit elevated numbers of trunk vertebrae compared to other species of *Liopholidophis* (Table 5). For females, these two species average about 10 more trunk vertebrae than the other species. Male *L. grandidieri* average about 10 more trunk vertebrae, and male *L. rhadinaea* about 20 more trunk vertebrae, than males of the other species. Thus, the smallest (*L. rhadinaea*) and one of the larger species (*L. grandidieri*) each show increases in trunk vertebrae compared with the other species.

DISCUSSION

Ontogeny of Sexual Dimorphism in *Liopholidophis sexlineatus*

Few studies have examined sexual dimorphism in neonatal snakes but body size (SVL) and tail length are sexually dimorphic in neonates of some species (e.g., Clark 1970; King et al. 1999; Klauber 1943; Krause and Burghardt 2007). Both characters are usually dimorphic in adults and, as a consequence, the significance of sexual dimorphism in snakes has been analyzed primarily with respect to adult morphology. Less attention has been devoted to the ontogeny of sexually dimorphic characters but these patterns appear to be species-specific (King et al. 1999). King et al. (1999) found two common patterns in the ontogeny of sexual differences in body size: sexual dimorphism present in the same direction in both neonates and adults or, alternatively, sexual dimorphism absent among neonates but present in adults. Only in rare cases was sexual dimorphism present in neonates but absent in adults, or in opposite directions in neonates and adults.

The two litters of *Liopholidophis sexlineatus* examined suggest that neonatal sexual size dimorphism is absent. Thus, the ontogeny of body size in this species (Table 1, Fig. 7) conforms to one of the common patterns found by King et al. (1999), although such small samples are not a powerful test because body size at birth could vary geographically or among litters. In contrast to body size, tail length is strongly sexually dimorphic at birth in *L. sexlineatus* (Fig. 2). Remarkably,

the degree of sexual dimorphism in tail length in neonatal *L. sexlineatus* (0.59, Lovich–Gibbons measure) is greater than any known neonatal dimorphism in snakes, and is greater than that observed in adults of most snakes (King et al. 1999; Klauber 1943). Such strong sexual dimorphism at birth is highly unusual among vertebrates (Badyaev 2002).

King et al. (1999) quantified the ontogenetic increase in sexual dimorphism using the absolute value of the difference between the neonate and adult indices of sexual dimorphism (ratio of the male to female means). Using this measure, the ontogenetic increase in sexual size dimorphism in *L. sexlineatus* (0.11) is less than that of four North American natricids, in which the indices were 0.12–0.29 (King et al. 1999). This pattern cannot be extrapolated to other species of *Liopholidophis* because closely related snakes can differ significantly in ontogenetic patterns, and interpopulational variation occurs in some species (King et al. 1999). Furthermore, *L. sexlineatus* is, along with *L. dolicocercus* and *L. varius*, among the least dimorphic of the species in adult size. The ontogenetic change in size dimorphism in *L. grandidieri* and *L. rhadinaea* may be considerably more because of their greater magnitude of adult SSD (Table 4).

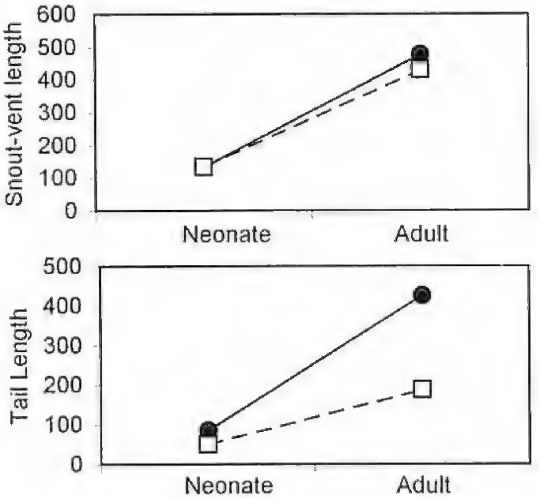


FIGURE 7. Ontogeny of body size (SVL) and tail length between neonatal and adult stages in *Liopholidophis sexlineatus*. Points are the mean SVL or tail length for neonates or adults, shown for each sex separately. Symbols: ● males, □ females.

The ontogeny of tail length dimorphism in *Liopholidophis sexlineatus* shows a more dramatic increase than body size between the neonate and adult stages (Table 4, Fig. 7). In addition to having an extraordinary degree of TLD at birth, the ontogenetic increase in TLD (0.15 using the difference measure of King et al. 1999) between neonates and adults is nearly twice the greatest change in four species of natricids (0.08; King et al. 1999), thus becoming the greatest reported values of this measure.

As might be expected from the general relationships between body size and tail length (Figs. 3, 5), the great magnitude of the ontogenetic increase in tail length dimorphism is primarily due to the strong positive allometry of the tail in males. Klauber (1943:32 and Table 9) computed indices of the ontogeny of relative tail lengths in 27 species of snakes (Colubridae, Dipsadidae, Lamprophiidae, Natricidae) based on the following formula, expressed as a percentage, separately analyzed for each sex:

$$(RTL_{Neonate} - RTL_{Adult})/½(RTL_{Neonate} + RTL_{Adult}),$$

where RTL is relative tail length. For male and female *L. sexlineatus* these coefficients were 33.8% and 2.5%, respectively. The male value is considerably greater than coefficients for any of the species tabulated by Klauber (1943) except males of *Phyllorhynchus decurtatus perkinsi* (34%); the male mean in Klauber's study was only 10.5%. The female coefficient for *L. sexlineatus* is less than the female mean in Klauber's study (3.6%). These comparisons show that the magnitude of sexual dimorphism present at birth and the extent of ontogenetic change between neonates and adults in *Liopholidophis sexlineatus* are exceptional.

Adult Sexual Dimorphism

Sexual size dimorphism (SSD) in *Liopholidophis grandidieri, L. rhadinaea,* and *L. sexlineatus* (Table 4) is high in comparison to other "colubrids" (Cox et al. 2007; Shine 1994a). In Shine (1994a), only 16 species had male-biased size dimorphism greater than or equal to the values shown by these species of *Liopholidophis* and of these, 14 were members of a single clade, the Colubridae (*sensu* Zaher et al. 2009); only three species had male-biased SSD greater than or equal to that of *L. grandidieri* and *L. rhadinaea*. These species of *Liopholidophis* are among the few tropical snakes in which male-biased sexual size dimorphism has been documented. Nonetheless, the generality of apparent patterns of SSD in "colubrids" (Shine 1994a) is as yet unclear because of the sampling bias toward temperate species and particular clades (Natricidae and Colubridae). In contrast to *L. grandidieri, L. rhadinaea,* and *L. sexlineatus*, indices of SSD for *L. varius* and *L. dolicocercus* are near the modal values for "colubrids" (Shine 1994a).

By any standards, tail lengths in male *Liopholidophis dimorphus, L. dolicocercus, L. grandidieri, L. rhadinaea*, and *L. sexlineatus* are exceptional (Table 1, Fig. 8). The mean and maximum male relative tail lengths in a survey of 110 species representing a broad sampling of "colubrids" were 29% and 65% of SVL, respectively (King 1989). A review of some systematic literature and my own unpublished data recovered only a few species in which male RTLs occasionally reach or exceed 70% of SVL. These include some individuals of *Ithycyphus blanci, I. miniatus*, and *Langaha madagascariensis* (Cadle, unpublished data) among other Malagasy snakes and, among Neotropical snakes, individuals of some species of the *Rhadinaea decorata* and *R. lateristriga* groups (Myers 1974), *Oxybelis aeneus* (Keiser 1974), and some species of *Chironius, Dendrophidion, Enulius, Leptophis, Pliocercus*, and *Scaphiodontophis* (Cadle, unpublished data; Oliver 1948; Henderson 1984; Savage and Slowinski 1996; Savage 2002). If snakes in which long tails are clearly associated with arboreality or anti-predator defense (specialized pseudautotomy) are eliminated from consideration, the exceptional tail lengths of *Liopholidophis* are even more remarkable (see below: Evolutionary Significance of SSD and Long Tails).

In all of the above cases except *Scaphiodontophis* (and perhaps *Pliocercus*), exceptional tail lengths apply to particular individuals with especially long tails rather than means for the species, thus emphasizing the unusually long tails in these five species of *Liopholidophis*. In contrast, the RTL of male *L. varius* (48% of SVL) is comparatively large but male tail lengths of this magnitude are found in many other "colubrids." The unusually long tails of males are the most striking characteristic of *Liopholidophis* but the tails of females are also comparatively long (mean RTLs 0.33–0.55; Table 1). These are greater than female RTLs in most "colubrids" (Klauber 1943; King 1989). Mean and maximum RTLs for females in King (1989) were 25% and 65% of SVL, respectively, and only two snakes had mean RTLs in females > 0.55 (*Leptophis ahaetulla* and *Psammophis schokari*).

The exceptional nature of relative tail lengths is emphasized by comparison with other "colubrids", which shows that male RTLs in *Liopholidophis* are unique (Fig. 9). Considering species with adult female RTL $\geq$ 0.33 (the minimum RTL of female *Liopholidophis*), mean RTLs for males and females are 0.46 and 0.42 in a geographically diverse sample representing several major lineages (Calamariidae, Colubridae, Dipsadidae, Homalopsidae, Lamprophiidae, Natricidae, Psammophiidae) (King 1989: Appendix). Corresponding means for *Liopholidophis* are 0.80 and 0.41. Thus, the mean RTL of female *Liopholidophis* is equivalent to the female mean of relatively long-tailed colubrids. Mean RTL in male *Liopholidophis* greatly exceeds the mean and, with the exception of *L. varius*, the maximum value, in a broad array of "colubrids" with comparatively long tails.

To a certain extent the unique body proportions of male *Liopholidophis* are more lizardlike

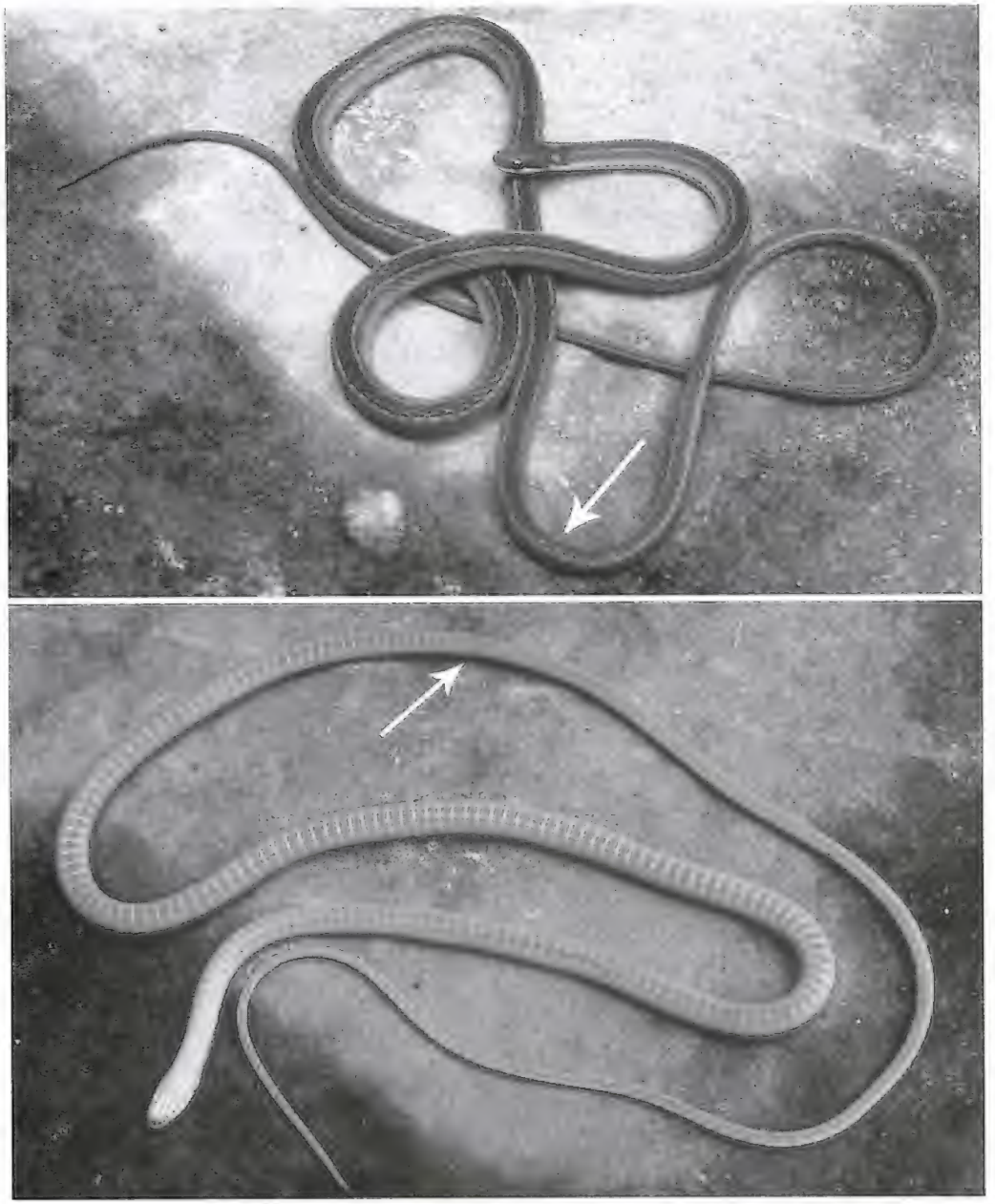


FIGURE 8. The male holotype of *Liopholidophis rhadinaea* (Museum of Comparative Zoology 180395; 412 mm SVL, 308 mm tail length) illustrating the extraordinary tail length attained by male *Liopholidophis*. The tail is 75% of SVL. Arrows indicate the proximal end of the tail. This species has the shortest relative tail length among the five species with long tails.

than snakelike. In surface-active lizards the tail comprises a substantial portion of the total length whereas in snakes the general pattern is for greater elongation of the body at the expense of the tail (Shine and Wall 2009). The repeated evolution of these patterns in squamates has been of long-standing interest and relates primarily to locomotory and digestive functions in burrowing versus terrestrial niches (Shine and Wall 2009; Wiens and Slingluff 2001; Wiens et al. 2006). Unlike most

limb-reduced lizards with exceptionally long tails (e.g., many anguids and pygopods), which are grass swimmers, this is an unlikely correlate for *Liopholidophis*. Within snakes, additional selective contexts for the evolution of longer tails include predator avoidance, arboreal habitats, and mating systems, which are considered below in greater detail (see Evolutionary Significance of SSD and Long Tails). The tails of male *Liopholidophis* do not attain the extreme lengths of many reduced-limbed, terrestrial lizards, in which the tail can be well over twice the SVL (Wiens et al. 2006). However, I am unaware of other snakes with RTLs approaching those of males of the long-tailed species of *Liopholidophis*, in which the tails are not associated with predator avoidance or arboreality, functions which do not appear to apply to *Liopholidophis*.

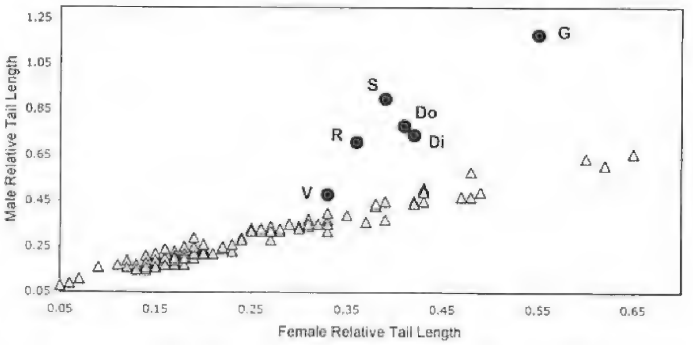


FIGURE 9. Bivariate plot comparing mean relative tail lengths of male and female *Liopholidophis* to a large sample of "colubrids" (Δ, compiled from King 1989: Appendix). Letters adjacent to data points for *Liopholidophis* indicate species, as follows: Di, *L. dimorphus*; Do, *L. dolicocercus*; G, *L. grandidieri*; R, *L. rhadinaea*; S, *L. sexlineatus*; V, *L. varius*.

Allometry of Tail Length in *Liopholidophis*

In most snakes the slope of the relationship between tail length and body size is greater in males than in females (King et al. 1999; Klauber 1943). In other words, for a given increase in body size, tails lengthen relatively more in males than in females. This pattern pertains to species of *Liopholidophis*, in which tail length is nearly isometric with SVL in females but positively allometric in males (Table 2 and Figs. 3, 5; intraspecific comparisons). The consistency of allometric patterns among species of *Liopholidophis* contrasts with some other snakes (e.g., *Thamnophis*), in which these patterns vary considerably among species (Shine et al. 1999).

Given the exceptionally long tails of male *Liopholidophis*, the slopes of the regressions of TailL on SVL for male *Liopholidophis* are, not surprisingly, greater than any previously reported. Klauber (1943: Table 12) reported slopes of 0.954 – 1.227 (mean = 1.097) for 14 species of "colubrids" and King (1989) found an overall slope of 1.15 for males of 104 species (56 genera). The allometric coefficients of female *Liopholidophis* average somewhat higher than those in Klauber's (1943) study (female slopes 0.969 – 1.147; mean = 1.043) and less than the overall female slope of 1.23 in King's (1989) study.

Vertebral Numbers in *Liopholidophis*

Sexual dimorphism in vertebral numbers in *Liopholidophis* reflects the patterns and unusual nature of size and tail length dimorphism. Male-biased sex disparity in the number of trunk vertebrae, as in *Liopholidophis* (Table 5), is unusual in snakes. In 255 species (315 populations) of snakes ("colubrids", elapids, and viperids), Shine (2000) found male-biased sex disparity in only 26% of cases in which the sexes differ in trunk vertebral number. The sex disparities in trunk vertebrae shown by *Liopholidophis* are greater than most of those found by Shine (2000), who recorded a maximum negative value of −18, the only one less than −10. Even more remarkable are the sex disparities in tail vertebrae. In Shine's (2000) sample, males had seven less to 17 more tail vertebrae than females, disparities much less than any species of *Liopholidophis*, in which males have

25 to 105 more tail vertebrae than females (Table 5). Thus, the magnitudes of disparities in both the trunk and tail vertebrae are very high compared to all other snakes sampled. Shine (2000) found a negative correlation between sex disparity in tail vertebrae and sex disparity in trunk vertebrae, although the correlation was positive in New World natricids. This correlation is nonsignificant in *Liopholidophis*.

Interspecific variation in vertebral numbers in *Liopholidophis* indicates the evolutionary basis of size differences among species. In vertebrates generally, elongation of the trunk is achieved either by an increase in segmental (e.g., vertebral) numbers, or by an increase in the size of individual segments (somatic growth) (Parra-Olea and Wake 2001; Wiens and Slingluff 2001). Despite strong differences in mean body sizes in comparisons by sex, *L. dolicocercus*, *L. sexlineatus*, and *L. varius* have similar numbers of trunk vertebrae (Table 5). This suggests that body size evolution has been accomplished by differential increases in segmental size, rather than differences in segmental numbers. On the other hand, *L. grandidieri* and *L. rhadinaea* exhibit increased vertebral numbers compared to other species, yet show divergent patterns of body size evolution: small (*L. rhadinaea*) versus large (*L. grandidieri*). High numbers of trunk vertebrae in caenophidian snakes (but not basal snakes; see Head and Polly 2007) tend to be correlated with large body size (Lindell 1994). In *Liopholidophis* the species with the greatest number of trunk vertebrae is also the smallest (*L. rhadinaea*; Tables 1, 5), but this species also has the lowest number of tail vertebrae among the five species with extremely long tails in males. These interspecific patterns suggest (1) that body size evolution within *Liopholidophis* is accomplished to some extent by both mechanisms common within vertebrates, and (2) that the evolution of segmental numbers in the body and tail are decoupled. The increased body segmental numbers in the diminutive species, *L. rhadinaea*, is consistent with the hypothesis that body elongation (in this case accomplished by increased vertebral numbers) in miniaturized squamates is an adaptation to maintaining minimum critical clutch sizes, given the functional constraints of neonate size and trunk volume in small adult females (Griffith 1990; Wiens and Slingluff 2001). *Liopholidophis rhadinaea* has clutch sizes of two to three eggs (Cadle 1996a; see later discussion herein), which is among the smallest known for oviparous Malagasy snakes.

Evolution of Sexual Dimorphism in *Liopholidophis*

Using different phylogenetic hypotheses, Cadle (1996a) and Glaw et al. (2007) interpreted the evolution of tail lengths, tail length dimorphism (TLD), and sexual size dimorphism (SSD) in *Liopholidophis*. Glaw et al. (2007) pointed out some broad areas of agreement with Cadle (1996a) but the two phylogenies actually suggest different scenarios if the evolution of these characters is relatively conservative, as explained below. In particular, they differ in their interpretations of the morphology of *L. varius* and *L. rhadinaea*, which have direct bearing on the evolution of sexual dimorphism in *Liopholidophis*.

By several criteria *Liopholidophis varius* (previously known as *L. pinguis*, as in Cadle 1996a; see Cadle 1998) is the most generalized species with respect to characters bearing on the evolution of TLD and SSD in *Liopholidophis*. The relative tail lengths of male and female *L. varius* are the least among species of *Liopholidophis* (Table 1), and regressions and analyses of covariance indicate that both sexes (but particularly males) have especially short tails compared to the other species with similar body sizes (Fig. 5). Tail length dimorphism in *L. varius* is less than any other species, including neonatal *L. sexlineatus* (Table 4). This species exhibits only marginally male-biased SSD, in contrast to all other species except *L. dolicocercus*, and these differences in size and tail length are reflected in the low disparities in vertebral numbers in *L. varius* (Table 5). Given

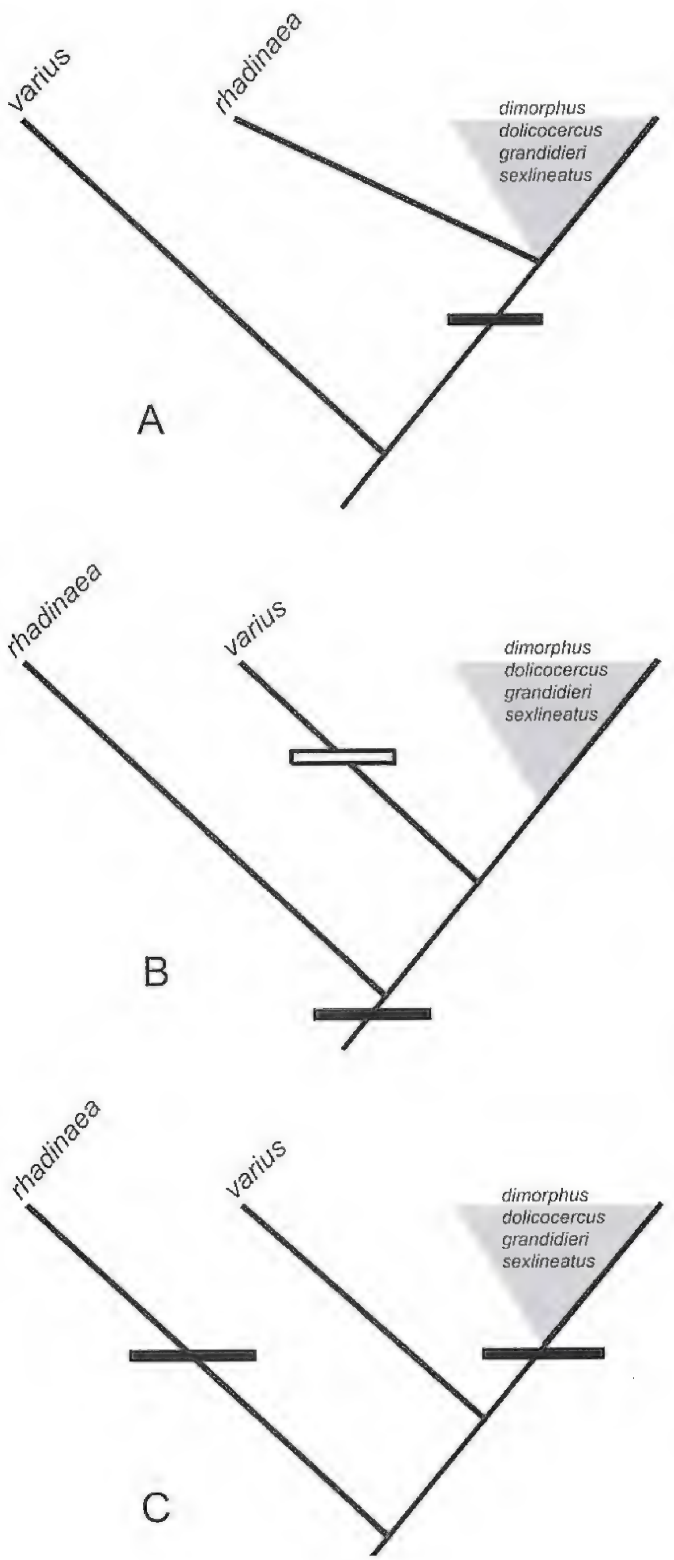
these distinctions, the phylogenetic position of *L. varius* is crucial to interpreting the evolution of these sexually dimorphic characters.

On the other hand, *Liopholidophis rhadinaea* is similar to the other long-tailed species with respect to tail morphology (i.e., *L. dimorphus*, *L. dolicocercus*, *L. grandidieri*, and *L. sexlineatus*), and to *L. grandidieri* with respect to SSD (Tables 1, 3; Fig. 5). The disparity between the sexes in the number of trunk vertebrae in *L. rhadinaea* is greater than any other species, whereas its disparity in tail vertebrae is comparable to that of other long-tailed species, and more than twice that of *L. varius* (Table 5). Unplanned multiple comparisons tests show that mean adjusted tail length in male *L. rhadinaea* is not significantly different from *L. dolicocercus*, and only marginally so from *L. sexlineatus*. In describing *L. rhadinaea*, Cadle (1996a) acknowledged its superficial resemblance in habitus and color pattern to some species of *Liophidium*. Nonetheless, extreme tail morphology, strong male-biased SSD, and derived characters of the skull support the association of *L. rhadinaea* with *Liopholidophis*, and it lacks derived dentition, dietary, and skull characters of *Liophidium* (Cadle 1996a:380–382; Cadle 1999:405).

As shown previously (Cadle 1996a) and expanded herein, the "extreme" conditions of male tail length and TLD (hereafter referred to as "extreme tail morphology") apply only to a subset of *Liopholidophis* species (i.e., all of the species except *L. varius*) (Table 1, Fig. 5). Extreme tail morphology can be defined by several criteria, including male relative tail lengths, the standardized residuals of the regression of tail length on SVL, and size-adjusted measures of TLD (RESULTS). Cadle (1996a), and subsequently Glaw et al. (2007), assumed that extreme tail morphology and male-biased SSD were derived characters.

The phylogenetic hypothesis of Cadle (1996a) for the five species then known, based on characters of TLD and color pattern, was the following: (*varius* (*sexlineatus* (*rhadinaea* (*dolicocercus*, *grandidieri*)))). According to this hypothesis, extreme tail morphology evolved once in the ancestor of the clade *sexlineatus-rhadinaea-dolicocercus-grandidieri* (Fig. 10A); *L. dimorphus*, described by Glaw et al. (2007), falls within this clade on the basis of its tail morphology and SSD (Table 1). In this model there is no homoplasy of extreme tail morphology. However, the evolution of extreme tail morphology is not strictly linear under this hypothesis because *L. sexlineatus* and *L. grandidieri*, the species with the longest relative tail lengths in males and greatest TLD (Tables 1, 3), are not sister taxa. *Liopholidophis dolicocercus*, hypothesized to be the sister taxon to *L. grandidieri* on the basis of detailed and unusual similarities in color pattern (Cadle 1996a), is similar to *L. rhadinaea* in the magnitude of its male relative tail length and in TLD (Table 4). These inferences led Cadle (1996a:454) to suggest that "if the degree of tail dimorphism has had a complex evolutionary history [i.e., was not a simple phylogenetic progression from short tails to extreme tail morphology], then hypothesizing that [*L. varius*] is the sister species to the rest of [*Liopholidophis*] on the basis of having the least tail dimorphism may be overly simplistic." Size dimorphisms can evolve very rapidly (Badyaev 2002) and empirical studies of sexually selected traits emphasize their evolutionary lability (Wiens 2001), so such complex patterns in *Liopholidophis* would not be unprecedented.

Cadle (1996a) made no inferences about SSD beyond concluding that male-biased SSD, an uncommon pattern in "colubrids," was a putative derived character supporting monophyly of the genus (= the "*Liopholidophis sexlineatus* species group" as it was known then). The varying degrees of SSD among species and the lack of demonstrable male-biased SSD in *L. dolicocercus* indicate that the evolution of SSD has not been a simple progression under the phylogenetic hypothesis of Cadle (1996a). Nonetheless, *L. varius* is only marginally sexually dimorphic in size and *L. rhadinaea* exhibits a degree of SSD second only to that of *L. grandidieri* (Table 4). These observations are consistent with a relatively basal phylogenetic placement of *L. varius* and a more



nested placement of *L. rhadinaea* if absence of SSD or female-biased SSD is plesiomorphic for the genus.

A legitimate criticism of Cadle's (1996a) phylogenetic hypothesis is that the assumed plesiomorphic states for SSD and TLD (stated above) strongly influence the resulting phylogeny. This creates an inherent circularity, in which the transformations of characters strongly affecting the tree topology is assumed to closely track the species phylogeny (De Queiroz 1996). This weakens the inference that *L. varius* is the sister

FIGURE 10. Scenarios for the evolution of extreme tail morphology in *Liopholidophis* according to two phylogenetic hypotheses; see text for explanation. The shaded triangle represents the clade comprising *L. dimorphus, L. dolicocercus, L. grandidieri,* and *L. sexlineatus* (i.e., species with extreme tail morphology except *L. rhadinaea*). Solid bars represent gains of extreme tail morphology; open bar represents loss. The assumed ancestral state in all cases is absence of extreme tail morphology. **A**, Cadle (1996a) hypothesized that *L. varius* was the sister taxon to other species of *Liopholidophis*. Under this hypothesis, the evolution of extreme tail morphology minimally occurred once in the lineage leading to the five species with extreme tail morphology. **B–C**, Glaw et al. (2007) hypothesized that *L. rhadinaea* was the sister taxon to all other species; they did not specify the phylogenetic position of *L. varius*, other than diverging later than *L. rhadinaea*. Under this hypothesis, the evolution of extreme tail morphology minimally requires two evolutionary changes, either: **B**, a gain and a loss (gain in the ancestor of the extant species of *Liopholidophis* and subsequent loss, or reversion to the ancestral condition, in *L. varius*); or **C**, two gains (once in *L. rhadinaea* and once in the common lineage leading to the other species with extreme tail morphology).

taxon to other species of *Liopholidophis* by virtue of having minimal TLD and SSD. Clearly, additional characters for phylogenetic analysis would ameliorate the effects of this bias.

Glaw et al. (2007) made steps in this direction by providing molecular data for three species of *Liopholidophis*, resolving their relationships as (*dimorphus* (*dolicocercus, sexlineatus*)). Among representatives of six other genera of Malagasy lamprophiids, they found moderately strong support for a sister-group relationship of *Liopholidophis* and *Liophidium* (however, two studies with different taxon and gene sampling found *Pseudoxyrhopus* and/or *Heteroliodon* as sister taxa to *Liopholidophis*, with *Liophidium* one node removed from these; Franzen et al. 2009, Vidal et al. 2008). Based on this finding, Glaw et al. (2007) asserted that *L. rhadinaea* was "the most basal *Liopholidophis*" based on the superficial similarities between *L. rhadinaea* and some species of *Liophidium* (Cadle 1996a). No molecular data were available for *L. grandidieri, L. rhadinaea,* or *L. varius*. Glaw et al. (2007) then proposed an "almost complete phylogenetic hypothesis for ... *Liopholidophis*, leaving only *L. varius* apart: (*rhadinaea*-(*dimorphus*-(*sexlineatus*-(*dolicocercus–grandidieri*)))))." Using this phylogeny, they hypothesized "... an allometric coevolution of snout-vent length and tail length that started early in the evolution of *Liopholidophis* and ... led from a small *Liophidium*-like ancestor without extreme dimorphism in tail length (and probably without male superiority [in SVL compared to females]) to the large *grandidieri* ...."

Scenarios for the evolution of sexually dimorphic characters in *Liopholidophis* proposed by Glaw et al. (2007) and Cadle (1996a) agree that the ancestral states in *Liopholidophis* most likely included absence of SSD or female-biased SSD, and absence of strong tail length dimorphism and exceptionally long tails in males. However, a basal position for *L. rhadinaea* based solely on its superficial similarity to some species of *Liophidium* and the curious omission of *L. varius* from consideration presents a more complex picture than suggested by Glaw et al. (2007). By setting aside *L. varius*, Glaw et al. (2007) failed to realize important implications of their scenario. If we accept the assertion that *L. rhadinaea* is the most basal species (Glaw et al. 2007), it follows that *L. varius* must be associated with the clade *dimorphus-sexlineatus-dolicocercus-grandidieri*, either the sister taxon to that clade or nested within it (Fig. 10B–C). Rather than a single origin and progressive allometric increase leading to extreme tail morphology from a small *Liophidium*-like ancestor, as suggested by Glaw et al. (2007), this phyletic pattern minimally requires two character state changes for the evolution of extreme tail morphology: either a gain of extreme tail morphology on the basal lineage of *Liopholidophis* and subsequent loss (reversal to the ancestral state) of this character complex in *L. varius* (Fig. 10B) (this scenario also applies if *L. varius* is nested within the clade represented by the shaded triangle); or two independent acquisitions of extreme tail morphology, once in *L. rhadinaea* and once in the lineage leading to the other species with this morphology (represented by the gray triangle in Fig. 10C). A similar evolutionary sequence applies to the evolution of male-biased size dimorphism.

Glaw et al. (2007) also suggested that two evolutionary trends were supported by their proposed phylogeny. First, that maximum total length and maximum SVL of males increased from *Liopholidophis rhadinaea* to *L. grandidieri*. Secondly, that relative tail lengths (RTLs) increased from *L. rhadinaea* to *L. grandidieri* in both sexes. However, maximum SVLs in both sexes occur in *L. dolicocercus*, not *L. grandidieri* (Glaw et al. 2007: Table 3 and Fig. 6A; Table 1 herein) and the trends are not consistent between males and females in comparisons of mean RTLs among species (Table 1). Moreover, these perceived trends are possible only by ignoring *L. varius*: SVLs are much greater in both sexes of *L. varius* compared to *L. rhadinaea* and RTL in male *L. varius* is much less than in *L. rhadinaea*. These patterns suggest more complex relationships between size and tail length than can be conveyed as a simple allometric progression starting with the premise that *L. rhadinaea* occupies a basal phylogenetic position.

In addition, other factors must be considered in analyzing phyletic trends in size-related parameters. Glaw et al. (2007) based their scenario on the largest specimens (in total length) of each species. However, because tail length scales positively with body size in male *Liopholidophis* (Figs. 3, 5) and the species differ in mean body size and adult size range (Table 1), using the largest specimens to model the evolution of total length or tail length can be misleading since both contain a measure of tail length. In such cases, statistical methods that account for size differences, e.g. regression (Fig. 5) or analysis of covariance (Table 3), are more appropriate. Despite significant tail length differences overall among species, for a given body size, tail lengths and relative tail lengths in male *L. rhadinaea* are comparable to those of *L. dolicocercus* and *L. sexlineatus* of similar size (its regression line falls between the last two; Fig. 5), are much less than *L. grandidieri*, and much greater than *L. varius*. Multiple comparisons tests confirm that the two species with the most distinctive adjusted tail lengths in males are *L. grandidieri* (significantly longer tail length) and *L. varius* (significantly shorter tail length); *L. rhadinaea*, *L. dolicocercus*, and *L. sexlineatus* have tails intermediate between these extremes. In the common regression of TailL on SVL for all males (all species), the standardized residuals of *L. rhadinaea* (mean = −0.127) are intermediate between those of *L. dolicocercus* (mean = −0.386) and *L. sexlineatus* (mean = 0.482), indicating that its tail length is also intermediate between the last two for individuals with similar SVL. The apparent lesser tail length of male *L. rhadinaea* suggested by Glaw et al. (2007) is an artifact of its overall small size and failure to consider *L. varius*.

The evolution of extreme tail morphology and male-biased SSD from a "*Liophidium*-like ancestor" also entails a consideration of these characters in *Liophidium*, which Glaw et al. (2007) did not address. In a sample of 12 males and 13 females representing eight species of *Liophidium* (Cadle, unpublished data), relative tail lengths ranged from 0.16 – 0.38 (mean = 0.29) for males and 0.13 – 0.29 (mean = 0.20) for females. The means are comparable to those in a survey of "colubrids" (means 0.29 and 0.25 for males and females, respectively; King 1989) but the means and all individual values for *Liophidium* are less than any in *Liopholidophis* (Table 1). For *Liophidium*, regression slopes of the relationship between tail length and SVL were 0.54 and 0.66 (males and females, respectively). These slopes were marginally not significantly different from 1.0 but a trend toward negative allometry is apparent, opposite the pattern in *Liopholidophis*. Sample sizes of *Liophidium* were too small to evaluate SSD, although trends were female-biased for the overall sample and individual species. Trunk vertebral numbers in *Liophidium* are highly variable (ranges for individual counts: 133 – 231 in males, 144 – 254 in females); numbers of tail vertebrae are low, reflecting their tendency toward short tails (ranges for individual counts, 41–63 in males, 34–68 in females). Despite small samples, the overall trend is for females having greater numbers of trunk vertebrae than males (opposite the pattern in *Liopholidophis*), whereas the opposite is true for tail vertebrae. The number of tail vertebrae in *Liophidium* is particularly low in comparison to *Liopholidophis* (Table 5).

Finally, it is not clear that small body size is plesiomorphic within *Liophidium*, as expected under the hypothesis of Glaw et al. (2007). *Liophidium* includes eight described and several undescribed species (Glaw and Vences 2007; Franzen et al. 2009). At least four species (*L. rhodogaster, L. therezieni, L. torquatum*, and *L. vaillanti*) can exceed 600 mm in SVL and several others exceed 400 mm SVL. These are within the size range of adults of the larger species of *Liopholidophis* and greater than typical body sizes of *L. rhadinaea* (Table 1). A recent phylogeny of most species of *Liophidium* (Franzen et al. 2009) resolved *L. rhodogaster*, one of the larger species, as the most basal divergence within the genus, and other large and small species with more nested divergences. Consequently, if *Liophidium* and *Liopholidophis* are sister taxa, it is unclear that the ancestral body size for either genus was especially small. These data suggest that a "*Liophidium*-like ancestor" for

Liopholidophis should have low RTL in males, isometric or negatively allometric relationship of tail length to body size, female-biased size dimorphism, very low numbers of tail vertebrae, and perhaps moderate to large body size.

Liopholidophis rhadinaea does not fit this profile and therefore is not a good model for a "*Liophidium*-like ancestor" with respect to the evolution of tail characters and body proportions within *Liopholidophis*. The similarities in overall size, habitus, and coloration between *L. rhadinaea* and some species of *Liophidium* are patently superficial, and occur in other diminutive snakes from Madagascar and other biogeographic regions (e.g., Cadle and Greene 1993; Guyer and Donnelly 1990; Vitt and Vangilder 1983). In fact, the specific epithet *rhadinaea* called attention to its strong resemblance in habitus, color pattern, and natural history to the Neotropical genus *Rhadinaea* (Cadle 1996a:374). Evaluation of body proportions and size in *Liophidium* reinforces the conclusion that characters in *L. varius* are more similar to putative ancestral states for *Liopholidophis* under the hypothesis of Glaw et al. (2007). Therefore, a basal divergence of *L. varius*, rather than *L. rhadinaea*, results in the most conservative evolutionary scenario of these characters (short male relative tail length, minimal TLD and SSD). However, until the phylogenetic positions of *L. rhadinaea* and *L. varius* are inferred with greater security, patterns of evolution of body size and tail length in *Liopholidophis* will not be clear.

Evolutionary Significance of SSD and Long Tails

Body proportions in snakes are subject to an array of selective forces related to locomotory performance, growth rates, predator-prey interactions, fecundity, and sexual selection (Arnold and Bennett 1988; Jayne and Bennett 1989; Krause et al. 2003; Lindell 1994, 1996; Shine 2000). Multiple, sometimes opposing, forces are probably operative in many instances and these vary over time and among populations and lineages (Madsen and Shine 1993b; Shine 2000). Thus, identifying the forces in particular cases requires detailed knowledge of ecology, which we lack for *Liopholidophis*. Nonetheless, we can make some predictions by analogy with snakes that are better known.

Body size and tail morphology are often considered together in the context of snake mating systems and intrasexual mate competition (e.g., Luiselli 1996; Shine 1993). However, I first consider the potential role of long tails in *Liopholidophis* in anti-predator defense, as occurs in some snakes (E. N. Arnold 1988). With respect to tail morphology, two patterns (not mutually exclusive) actually need explanation. The first is the evolution of long tails *per se* (both male and female *Liopholidophis* have unusually long tails), which is potentially associated with antipredator defense (long tails are also associated with arboreality but there is no indication of arboreal proclivities in any species of *Liopholidophis*). The second is the evolution of sexual dimorphism in tail length, which is probably related to mating systems.

Unlike some snakes with very long tails (e.g., Savage and Slowinski 1996), the tails of *Liopholidophis* are not inordinately fragile and do not appear to be specialized for breakage. Tail breakage frequencies for species of *Liopholidophis* are comparable to many other snakes with much shorter tails (0 – 25%; Cadle 1996a:446; Cadle, unpublished data), and are less than in many snakes with both unspecialized and specialized pseudautotomy (e.g., *Coniophanes fissidens*, *Pliocercus*, and *Scaphiodontophis*, in which tail breakage frequencies are 50–80% among adults; Mendelson 1992; Savage and Crother 1989; Savage and Slowinski 1996). Most of the long-tailed snakes compared above to *Liopholidophis* (see Tail Length and Tail Length Dimorphism in Adults) have high tail breakage frequencies and the tails appear to be anti-predator adaptations (Savage 2002). Furthermore, in snakes with specialized pseudautotomy such as *Pliocercus* and *Scaphiodon-*

tophis, in which the extraordinary tail lengths are primarily anti-predator adaptations, tail lengths and segmental counts are not sexually dimorphic except in some portions of the geographic ranges (Savage and Crother 1989; Savage and Slowinski 1996).

In contrast, males do not predominate among specimens of *Liopholidophis* with broken tails, as might be expected if their inordinately long tails incur greater risk of breakage than the shorter tails of females. *Liopholidophis varius*, the species with the shortest relative tail length, had the highest frequency of broken tails and all of those individuals were females (Cadle 1996a:446). These observations suggest that anti-predator defense plays an insignificant role, if any, in the evolution of long tails in *Liopholidophis*. Furthermore, the relatively low frequencies of tail breakage (compared to other snakes with pseudautotomic tails) suggest that the tails in *Liopholidophis* species are not pseudautotomic.

On the other hand, male-biased size and tail length dimorphisms are related to mating systems in some snakes. Male-biased size dimorphism is usually associated with male-male competition for mates (Rivas and Burghardt 2001; Shine 1978, 1993, 1994a), which may include combat encounters or more subtle effects during courtship and mating. For species in which multiple males simultaneously court females, larger males have advantages over smaller males in maintaining positions for mating (male-male interaction) (Luiselli 1996; Madsen and Shine 1993a; Shine et al. 1999, 2000) and larger male size facilitates forcible copulation (male-female interaction) (Shine and Mason 2005). In some snakes (e.g., *Thamnophis sirtalis*) males with longer tails have longer hemipenes and obtain more matings than males with shorter tails, in part due to the advantages of long tails during tail wrestling among males (Shine et al. 1999; Shine 2000). Thus, sexual selection may affect body size and relative tail size.

King (1989) tested predictions of three hypotheses for the effects of selection on tail length in "colubrids": (1) morphological constraint (in relation to the space needed to house hemipenes and their retractor muscles in males); (2) female reproductive output (body size relative to female reproductive output and the relationship between SSD and TLD); and (3) male mating ability (in relation to the use of the tail in copulatory attempts and in thwarting competing males for mates). The morphological constraint and female reproductive output hypotheses were generally supported but some predictions of each hypothesis were not fulfilled and intraspecific comparisons for *Nerodia sipedon* failed to support any of the hypotheses. King's (1989) tests may have been too insensitive to detect effects of male mating ability, which subsequently found support in *Thamnophis* (Shine et al. 1999).

For *Liopholidophis* we have neither the requisite natural history data nor sufficient samples for analysis of intraspecific variation of the significance of tail length. The unusually long tails in male *Liopholidophis* seem unlikely to be solely related to size of the hemipenes (morphological constraint) because it is not clear that tail lengths above a certain size are needed simply to house larger hemipenes. Hemipenes and associated anatomy are expected to impose greater constraints on minimum tail length in short-tailed snakes (King 1989). Also, many snakes with much shorter tails have larger hemipenes than species of *Liopholidophis*. Cadle (1996a) remarked that the hemipenes in *Liopholidophis* were small compared to many snakes with shorter tails, although such interspecific comparisons can mask intraspecific variation in hemipenial size related to individual mating success. Nonetheless, it is unlikely that hemipenial size alone explains the evolution of such long tails in *Liopholidophis*.

King (1989) found a negative interspecific correlation between tail length dimorphism and body size dimorphism, i.e., species with more male-biased TLD tend to have greater female-biased size dimorphism. In *Liopholidophis* tail length and body size are male-biased in general, with three species (*L. grandidieri*, *L. rhadinaea*, and *L. sexlineatus*) exhibiting a strong male bias in both

parameters. These patterns are inconsistent with predictions concerning the relationship between TLD and SSD based on selection for female reproductive output (King 1989), as are the estimates of relative clutch mass for *L. sexlineatus* (0.38), which are not especially high by snake standards (Dunham et al. 1988; King 1989). However, *L. sexlineatus* is semiaquatic, which could influence its reproductive effort because aquatic snakes in general have lower reproductive efforts than terrestrial snakes (Shine 1988); unfortunately, we currently have no objective measure of the extent to which *L. sexlineatus* is aquatic.

Thus, male-biased size dimorphism and strong tail length dimorphism in *Liopholidophis* are most likely associated with male-male agonistic interactions and/or male-female mating behaviors. I predict that further study will discover evidence of such behavior. A corollary is that the variation in tail length among males within species of *Liopholidophis* should be reflected in individual mating success. Range-wide variation in tail length among male *L. sexlineatus* is substantial and is greater than variation among females (RESULTS). However, we do not yet know the extent to which this variability is reflected at the level of populations. It is also possible that male-biased size dimorphism in *Liopholidophis* is incidental to selection on tail length or vice versa, as has been shown in *Thamnophis* (S.J. Arnold 1988; see also Lindell 1994). However, the effects of selection depend on the genetics of body proportions and the magnitude of selection coefficients. There is no reason to expect similar genetic correlations among disparate taxa.

An alternative to the male mating success hypothesis proposed by Glaw et al. (2007) is that female choice explains the long tails of male *Liopholidophis*. However, current consensus based on theory, behavioral observations, and paternity data is that female choice is rare in snakes (Cox et al. 2007; Duvall et al. 1992; Duvall et al. 1993; Garstka and Crews 1985; Shine 2003; Shine and Mason 2001; Shine et al. 1999; Shine et al. 2003; Uller and Olsson 2008; Voris et al. 2008). A form of female choice based on the response of males to elevation of the female's head during courtship (a measure of male success in combat behavior) has been observed in *Agkistrodon contortrix* and *Boiga irregularis* (Duvall et al. 1993; Greene and Mason 2000; Schuett and Duvall 1996). Neither male nor female tails are involved.

Other behaviors have an unknown or ambiguous relationship to female choice. Female-initiated axial rotations that interrupt copulation have been observed in *Thamnophis* (Perry-Richardson et al. 1990; Shine et al. 2003), but the cues responsible for this behavior and whether it constitutes a form of mate choice have not been determined. Multiple paternity pertains to a high percentage of clutches in snakes (Rivas and Burghardt 2005; Uller and Olsson 2008), which is consistent with several forms of mate choice. However, research has failed to demonstrate that females choose mates with particular overt phenotypic characteristics; postcopulatory cryptic female choice (i.e., female control of fertilization by different males) has been documented in only one small and highly inbred population of *Vipera* (Madsen et al. 1992; Shine 2003). Instead, a combination of mate-encounter frequency rates and benefits to males, rather than female choice, probably leads to multiple paternity (Madsen et al. 1992; Rivas and Burghardt 2005; Shine 2003; Shine et al. 2003; Uller and Olsson 2008).

Glaw et al. (2007) provided no observations to support the claim that female choice is the selective force behind the evolution of long tails in male *Liopholidophis* and no data on other snakes is supportive by analogy. Nonetheless, female choice is often difficult to demonstrate or distinguish from other mating tactics (Eberhard 2004) and is a possibility in some snakes (Rivas and Burghardt 2001; Shine and Mason 2005; but see Shine et al. 2003). Tail searching and attempts at intromission by males during courtship (Carpenter 1977; Gillingham 1977, 1987) are potential avenues for overt or cryptic female choice based on tail characteristics, perhaps analogous to cryptic female choice based on sire size in *Anolis* lizards (Calsbeek and Bonneaud 2008). No evidence

exists for such a phenomenon in snakes and whether it is a possibility depends on other mating parameters (e.g., number of competing males for mating opportunities). Thus, strong inferences for poorly known species, such as *Liopholidophis*, are not possible. Nonetheless, male-male mate competition and agonistic behavior and/or size advantages of males interacting with females during courtship remain the most likely explanations for male-biased size dimorphism and the exaggerated tail length in male *Liopholidophis*.

Other life history variables also correlate with patterns of sexual size dimorphism in snakes. Viviparity results in a shift of SSD toward larger female size, probably due to fecundity selection (Shine 1994a). *Liopholidophis sexlineatus* is the only confirmed viviparous species of *Liopholidophis* and its size dimorphism is less than that of *L. grandidieri* and *L. rhadinaea*, which are known to be oviparous (Cadle 1996a). These observations are consistent with selection for larger body size in females (and consequently, less size dimorphism) in *L. sexlineatus*, and could help explain the apparently nonlinear evolutionary patterns of SSD noted above. However, of the other species with little SSD, the reproductive mode of *L. varius* is unknown and *L. dolicocercus* is probably oviparous (see below). In any case, except for vipers and elapids, viviparous "colubrids" with male-biased SSD are rare (Shine 1994a).

Sexual Dimorphism and Ecology in *Liopholidophis*: Questions for Further Research

The unusual nature of sexual dimorphism in *Liopholidophis* calls for explanation but understanding the allometry of tail length is only a preliminary step. Positive allometry of sexually selected traits will tend to evolve under conditions in which fitness depends on a combination of trait size and body size, such that a greater relative advantage of trait size pertains to larger individuals (Bonduriansky 2007; Bonduriansky and Day 2003). However, the existence of positive allometry is insufficient to infer selection dynamics because similar allometric patterns can result from different selective regimes. Ecological and functional studies of *Liopholidophis* should relate body size and tail length to the fitness of individuals so that the effects of natural and sexual selection can be measured.

Further study of the ontogeny of sexual differences in body size and size at sexual maturity in *Liopholidophis* is crucial because understanding their causes depends on the life history stages at which they are manifested. I made assumptions about size at sexual maturity, which affects calculations of mean adult body sizes and measures of size dimorphism derived from them. These estimates need greater precision, especially for males. Current evidence suggests that sex differences in age-specific growth rates and patterns (and hence, differential energy allocations to growth, maintenance, and reproduction) are the proximate factors producing most patterns of sexual size dimorphism in squamates (Cox et al. 2007; John-Alder and Cox 2007; John-Alder et al. 2007). My analyses are based on cross-sectional allometry, so that the relationship of these patterns to the ontogeny of individuals and age-specific patterns in males and females is ambiguous (Cock 1966). In other words, we don't know how like-aged male and female *Liopholidophis* differ in size, proportions, or rates of growth and survival. Two observations suggest that growth of the tail and body are decoupled: male *L. sexlineatus* (and probably the other species) with the longest tails span nearly the entire adult size range, and interspecific patterns of vertebral variation are not concordant between the body and tail (RESULTS). Study of the ontogeny of sexual differences should attempt to pinpoint when they develop with respect to age and environmental influences (e.g., food availability).

The presence of strong sexual dimorphism in tail length from birth in *Liopholidophis sexlineatus* suggests that proximate mechanisms for TLD act in early development. These might include

sex-biased hormonal or maternal influences, sex differences in duration of developmental stages, or interactions among these factors (Badyaev 2002). Hormones mediate neonatal sexually dimorphic head proportions in some snakes (Shine and Crews 1988). However, similar sexually dimorphic phenotypes can be produced by hormonal pathways that differ dramatically between closely related species (Cox et al. 2007; John-Alder and Cox 2007; John-Alder et al. 2007; Rhen 2007). These mechanisms are open to experimental manipulation and can provide insight into the proximate means of achieving sexually dimorphic differences.

Some functional questions can only be answered with experiments and additional field observations. Research on mating systems, including courtship behaviors and interactions within and between members of each sex, and studies of locomotory performance addressing the relevance of sexually dimorphic tail morphology are critical. Parallel studies of mating and locomotory performance would help tease apart sexual and natural selection on tail morphology. Based on the existence of male-biased size dimorphism, agonistic interactions are likely to occur among males but this needs confirmation. Body size and tail length variation, and the use of tails by males during mating and agonistic encounters needs study in relation to mating success. Locomotory performance depends on interactive effects between relative numbers of body and tail vertebrae (Arnold and Bennett 1988). Hence, the performance of male and female *Liopholidophis* is of special interest in view of their extraordinary differences from one another and from other snakes.

Individual and geographic components of variation in tail morphology need to be correlated with other aspects of morphology (e.g., variation in hemipenial size; Shine et al. 1999). The sample of *Liopholidophis sexlineatus* analyzed here is drawn from throughout the species' range, but many specimens (11 of the adult sample) come from the Ambatolahy population, which also provided the neonatal samples analyzed. Because patterns of sexual dimorphism vary among populations (e.g., Pearson et al. 2002; Pizzatto and Marques 2006; Thorpe 1989), future work should evaluate the generality of the patterns elucidated here with particular attention to geographic variation. Finally, a comprehensive and well-supported phylogeny including all species of *Liopholidophis* is needed to interpret character evolution and to resolve competing models for the evolution of sexually dimorphic characters.

Unfortunately, most species of *Liopholidophis* are apparently uncommon so that critical observations are likely to be serendipitous. However, *L. sexlineatus* is widespread, which makes it ideal for assessing geographic variation in morphology, behavior, and natural history. Also, it can be locally abundant (encounter rates up to 10 or more per hour) and occurs in open habitats (e.g., rice paddies), which facilitates field observation. Because *L. sexlineatus* is viviparous, naïve individuals for experiments of feeding, locomotion, and antipredator behaviors are easily obtained, and study of phenotypic plasticity in sexually dimorphic characters due to maternal, ecological (e.g., dietary), or endocrine effects during development is facilitated (Krause and Burghardt 2007; Osypka and Arnold 2000). Laboratory and field studies of this species could shed light on the significance of the extraordinary sexual dimorphism and variation in reproductive mode within these snakes.

Ecological Correlates of Viviparity in Malagasy Lamprophiids

Confirmation of viviparity in *Liopholidophis sexlineatus* brings to three the number of species of Malagasy lamprophiids known to be viviparous. In addition to *L. sexlineatus*, live birth has been observed in captive specimens of *Stenophis citrinus* (Vences et al. 1998) and *S. pseudogranuliceps* (Mertens 1955; Vences et al. 1998) (*Stenophis* includes approximately 12 species, sometimes placed in *Lycodryas*; see Cadle 2003:1000–1001). *Liopholidophis* is also the only genus of Malagasy lamprophiids for which both oviparity and viviparity can be considered confirmed. Cadle

(1996a) inferred that *L. grandidieri* and *L. rhadinaea* were oviparous based on females containing oviductal eggs with embryos in Dufaure-Hubert stages 27–30 and covered by leathery, mineralized eggshells (most squamate eggs are laid between stages 26 and 33; Andrews and Mathies 2000; Shine 1983a). With some equivocation, Cadle (1996a) also inferred oviparity in *L. dolicocercus* based on the presence of "shelled" oviductal eggs (but no discernible embryos) in two females. Further details were not reported at that time, but these eggshells were thick, opaque, and white, indicating that the calcareous layer of the shells had been laid down (Packard and DeMarco 1991). Since the crystalline layer is not deposited in viviparous squamates (Blackburn 1993; Packard and DeMarco 1991; Packard et al. 1977; Weekes 1935), oviparity in *L. dolicocercus* can reasonably be assured.

Vences et al. (1998) inferred that *Stenophis carleti* was oviparous based on a communication from Charles Domergue, who reported "a dissected female ... that contained 4 eggs of 43 × 8 mm." However, without details concerning the shell membranes (e.g., whether a crystalline layer is present) or developmental stages of oviductal eggs, inferring reproductive mode solely from the presence of "eggs" is problematic (Blackburn 1993). Moreover, recent evidence based on a sample of two species suggests that *Stenophis* is not monophyletic (Vidal et al. 2008) (reproductive mode is known for only one species in that study). Thus, the existence of dual reproductive modes in "*Stenophis*" (or monophyletic subclades thereof) needs confirmation.

Species or genera in which oviparity and viviparity co-occur offer the best cases for elucidating the ecological correlates and ultimate causes of the evolution of viviparity (Packard et al. 1977; Qualls and Shine 1998). Present knowledge precludes a rigorous analysis of these factors in *Liopholidophis* but we can take preliminary steps by comparing the three viviparous lamprophiids from Madagascar. At one level they have little in common. *Liopholidophis sexlineatus* is semiaquatic and distributed in the eastern rainforests and central highlands from 500–2500 m elevation; its biotope is humid, moderately seasonal, and has an abbreviated dry season that can be quite cool. *Stenophis citrinus* and *S. pseudogranuliceps* are slender arboreal snakes inhabiting lowland (< 1000 m) dry deciduous forests in western Madagascar (Glaw and Vences 2007); known localities are arid, with strongly seasonal rainfall, an extended dry season, and warm temperatures year round (from environmental summaries in Nicoll and Langrand 1989). *Liopholidophis* and *Stenophis* are only remotely related within the Malagasy lamprophiid radiation (Nagy et al. 2003; Vidal et al. 2008).

Liopholidophis sexlineatus apparently differs from its congeners in several aspects of natural history but few observations have been reported for *L. dimorphus*, *L. dolicocercus*, and *L. grandidieri*; virtually nothing is known about *L. varius* because its geographic distribution is poorly circumscribed and even basic information such as habitat have not been reported (Cadle 1996a; Glaw and Vences 2007). *Liopholidophis sexlineatus* is the only semiaquatic species and the only one inhabiting open habitats; the other species inhabit pristine rainforests and are fully terrestrial with the possible exception of *L. varius* (one of the few known localities for *L. varius* comprises the largest area of freshwater ecosystems in Madagascar). *Liopholidophis sexlineatus* is the most widely distributed species and holds the altitudinal record for Malagasy snakes, 2498 m (Chiari et al. 2006), at a locality that experiences cool conditions in summer and winter (Vences et al. 2002). The other species have more restricted distributions, geographically and elevationally: *L. dimorphus* (300 m), *L. dolicocercus* (800–1200 m), *L. grandidieri* (1200–1400 m), *L. rhadinaea* (900–1100 m), *L. varius* (900–1000 m); Glaw and Vences (2007) provide recent summaries of distributions.

Research on reproductive modes in squamates emphasizes the overwhelming role of cold climates (high latitudes or elevations) in promoting the evolution of viviparity (Andrews 2000; Shine 1983b, 1985, 1987, 2004b). Tinkle and Gibbons (1977) thought that environmental unpredictabil-

ity, of which cold climates are one example, correlated with most cases of squamate viviparity (see also Shine 1985). For example, arid environments are unpredictable with respect to eggs within a nest because desiccation could overtake eggs before hatching, thus favoring viviparity in which the female has more control over the hydric environment of her developing young (Weekes 1935). Shine (2002b) rejected this hypothesis for one study system based on the thermal environments of nests but its generality is not yet clear. Both thermal and hydric environments have strong phenotypic effects on offspring traits relevant to fitness (e.g., Andrews 2004; Arnold and Peterson 1989; Brown and Shine 2004, 2006a; Rhen and Lang 2004; Shine 2003; Shine and Brown 2002b; Shine et al. 1997). Shine (1995) generalized the cold climate hypothesis, suggesting that viviparity evolves because females can manipulate the thermal conditions of their developing young, thereby incurring selective advantages by enhancing their offspring's phenotypes. Shine's 'maternal manipulation hypothesis' has received empirical support (Shine 2004a; Webb et al. 2006) and could operate in many circumstances with differing selective pressures.

Viviparous Malagasy lamprophiids exhibit several ecological traits implicated in the evolution of squamate viviparity (Tinkle and Gibbons 1977): aquatic environments and high elevations (*Liopholidophis sexlineatus*); and arid environments and arboreality (*Stenophis* species). These correlates seem to have little generality (Shine 1985; Shine and Bull 1979; Tinkle and Gibbons 1977) but could still be relevant to specific cases. They also suggest some tests for the evolution of viviparity in *Liopholidophis* and *Stenophis*. For example, if cold climates were the driving force for the origin of viviparity in *L. sexlineatus*, the cold climate hypothesis predicts an intraspecific phylogeographic pattern in which high-elevation populations are basal and lower elevation populations more nested within an intraspecific phylogeny. This test is weak, however, because failure to find this pattern does not negate the cold climate hypothesis: ancestral phylogeographic patterns can be erased by specific patterns of extinction or dispersal. The cold climate hypothesis is less easily applied to the cases of viviparity in *Stenophis* because all but perhaps one species occur only at low and mid-elevations (<1100 m). Reproductive modes of most species are unknown and their natural history is poorly understood (Glaw and Vences 2007). However, because hydric environments have profound effects on offspring phenotypes (Brown and Shine 2006a), the arid environments experienced by viviparous species of *Stenophis* may be relevant.

More research on the physiological ecology of eggs, nests, and pregnant versus non-pregnant females, and the relationship between developmental environments and offspring phenotypes would further our understanding of viviparity in *Stenophis* and *Liopholidophis*. Special attention to the thermal and (particularly in *Stenophis*) hydric environments would be fruitful avenues for research, and are critical to testing hypotheses about the ecological and evolutionary significance of squamate reproductive modes (Andrews 2004; Shine 2002a). These questions present formidable challenges but their answers will further our understanding of the evolution of viviparity in Malagasy snakes.

Reproductive Biology of Malagasy Snakes: What Do We Really Know?

This discussion of reproductive modes in *Liopholidophis* and *Stenophis* highlights important gaps in basic knowledge of Malagasy "colubrid" life histories. Despite an enormous increase in knowledge of the natural history of Malagasy reptiles (Goodman and Benstead 2003; Glaw and Vences 2007), the reproductive biology of Malagasy snakes is poorly documented. A summary of the current state of knowledge can serve as a stimulus for further research. As Blackburn (1993) emphasized, much confusion and ambiguity in the inference of squamate reproductive modes has arisen from imprecisely reported or poorly documented observations. I here summarize the litera-

ture on the reproductive biology of Malagasy lamprophiids and psammophiids, evaluate the reliability of the inferred reproductive modes using Blackburn's (1993) framework, and suggest ways for improving our knowledge in this area.

Table 6 summarizes the reproductive biology of Malagasy lamprophiids and psammophiids and shows that we have only fragmentary knowledge of basic reproductive parameters for less than one-third of the approximately 80 species. Most data are based on very small samples, often only one or two observations. Of the species for which reproductive mode has been inferred, the reliability is moderate to weak in about one-third of the species, i.e., reliability ≤ 3 using Blackburn's criteria (1993: Table 2). No data are available for any species of *Brygophis, Compsophis, Exallodontophis, Heteroliodon, Liophidium, Pararhadinaea*, or *Pseudoxyrhopus*, which together account for more than one-third of the species in Madagascar.

Some descriptions in the literature are ambiguous without additional details. For example, Domergue (1984) stated that a specimen of *Alluaudina bellyi* contained five eggs "which have thin shells; two eggs were studied, one ... with the embryo already well-formed, the other ... [with no distinguishable embryo]." Either viviparity or oviparity could be consistent with this statement depending on the stage of development of the embryo and the meaning of "thin shell." Thin shell membranes are present in many viviparous squamates and in oviparous squamates early in the formation of the eggshell (Blackburn 1993; Packard et al. 1977), and embryos are retained through a significant portion of development even in oviparous species (Andrews and Mathies 2000). Glaw and Vences (2007) reduced Domergue's statement to the equally ambiguous, but less informative, "a dissected female contained five eggs." Is *A. bellyi* oviparous or viviparous? The information content of these observations could be enormously increased with little effort. Greater precision in reporting the reproductive characteristics of Malagasy snakes and careful attention to the reliability of inferences (Blackburn 1993) would considerably advance our understanding of this radiation.

Two general patterns emerge from Table 6. First, females are gravid and observations of oviposition or birth in Malagasy lamprophiids/psammophiids are concentrated in the wet season (December to March) or early dry season (April to June). A few observations of oviposition in October and November could reflect lengthier reproductive seasons in those species or year-to-year variation in the onset of conditions conducive to reproduction. An exception to this pattern seems to be *Langaha madagascariensis*, for which six reported clutches were laid between August and

Notes for Table 6:

*The following types of reports were excluded because of their inherent ambiguity: unsupported statements of reproductive mode; imprecise statements (e.g., "female contained eggs"); and reports of ovarian eggs only. Reports of oviductal "eggs" are included if they provide data on clutch size or season. Seasonal data for clutches laid in captivity are excluded unless it is clear that they derive from field-collected gravid females that oviposited after a short time in captivity.

Observations: 1, Wild caught gravid female laying eggs or giving birth in captivity; 1a, Captive breeding and egg-laying; 1b, Field collected eggs with delayed hatching in captivity or with identifiable embryos, or females observed laying eggs in the field. 2, Dissected female with "thin envelope having well-formed embryos." 3, Dissected female with oviductal eggs covered by a thick leathery shell and confirmed embryos in Dufaure-Hubert stages 25–30. 4, Dissected female with oviductal eggs having thick, opaque (calcareous) eggshells but no embryos detected or not reported. 5, Shelled oviductal eggs not examined for embryos. 6, Enlarged oviductal eggs determined by palpation through the body wall only or unsupported statement referring to "eggs."

Seasonal Data: B, births or hatching of eggs. E, Eggs laid in captivity. EFld, Eggs found in nests in the field; identity verified from hatchlings or advanced embryos. FC, female carrying oviductal eggs.

References: 1, Baldwin 1999. 2, Cadle 1996a. 3, Cadle 1996b. 4, J.E. Cadle, unpublished data. 5, this paper. 6, Campbell and Murphy 1977. 7, Conant 1938. 8, Domergue "1972" [1973]. 9, Domergue 1984. 10, Domergue 1986. 11, Domergue 1987. 12, Domergue 1988. 13, Domergue 1993. 14, Domergue 1994. 15, Glaw and Vences 2007. 16, Kreutz 1989. 17, Mertens 1955. 18, Mori 2002. 19, Mori and Tanaka 2001. 20, Preston-Mafham 1991. 21, Reams 1999. 22, Vences et al. 1998.

TABLE 6. Summary of reproductive parameters for Malagasy lamprophiids and psammophiids. Keys to Observations, Seasonal Data, and References are given on the preceding page. Reliability criteria are from Blackburn (1993: Table 2).*

Species	Reproductive mode	Observations	Reliability criterion	Clutch size	Seasonal data	References
Alluaudina bellyi	?	2	0, P (see text)	5	—	9
Dromicodryas bernieri	Oviparous	1b	5, B	3–5	EFld, January	4
Dromicodryas quadrilineatus	Oviparous	1b	5, B	—	—	15, 20
Ithycyphus miniatus	Oviparous	4–5 ?	3, K	5	FC, December	10
I. perineti	Oviparous	1	4–5, F, C	7	E, 9–10 December	10, 15
Langaha madagascariensis	Oviparous	1	4–5, F, C	5–12	E, 22 August –2 Nov. B, 22 December–7 Jan.	1, 15, 21
L. pseudoalluaudi	Oviparous	1	4–5, F, C	3	E, October	12
Leioheterodon madagascariensis	Oviparous	1, 1a	4–5, B, F	10–13	E,1 November	6, 7, 15, 19
Liopholidophis grandidieri	Oviparous	3	3, K	4–5	FC, January	2, 4
L. dolicocercus	Oviparous	4	3, K	5–7	FC, December-January	2, 4, 5
L. rhadinaea	Oviparous	3	3, K	2–3	FC, December-January	2
L. sexlineatus	Viviparous	1	4, E	4–12	B, March–April FC, 23 December	2, 5
Madagascarophis colubrinus	Oviparous	1, 1b	5, B–C	2–8	E, 15 Oct EFld, 13 January	4, 6, 11
Micropisthodon ochraceous	Oviparous	1	5, C	10	E, early May	13
Mimophis mahfalensis	Oviparous	1, 1b	5, B	5	E, 11 November EFld, 2 November	17, 18
Stenophis carleti	?	6	0, P (see text)	4	—	15, 22
S. citrinus	Viviparous	1	4, E	2	B, late December	22
S. pseudogranuliceps	Viviparous	1	4, E	1–4	B, end of January	17, 22
Thamnosophis epistibes	Oviparous	1, 4	3–5, C, F, K	3–6	E, December FC, 5–10 January	2, 4, 8
T. infrasignatus	Oviparous	3, 1	3–5, C, F, K	5–9	E, end Nov.; end March FC, 1–13 January	2, 4, 8, 15
T. lateralis	Oviparous	1	5, C	4–13	E, November-December FC, 16–19 December	4, 8, 15, 16
T. stumpffi	Oviparous ?	6	0, Q	4	—	2

October (late dry season) and hatched in late December to early January (early wet season). Unlike most Malagasy snakes, this widespread species occurs in both wet and dry forest (Glaw and Vences 2007); the pattern of late dry season oviposition could reflect a similarly broad ecological amplitude of this species or its eggs. Secondly, data on clutch sizes indicate that Malagasy species are generally similar to other snakes (clutch sizes of 2–16 are found in most snakes; Fitch 1970). The diminutive terrestrial snake *Liopholidophis rhadinaea*, and slender arboreal snakes in the genera *Langaha* and *Stenophis* tend to have the smallest clutch sizes (2–4). These associations of clutch sizes with ecological and size variables are expected based on general patterns within snakes (Fitch 1970).

The apparent strong seasonality of reproduction in Malagasy snakes also applies to Malagasy lizards and turtles (Glaw and Vences 1996), and is similar to most other tropical squamates (Shine 2003). The factors mediating seasonality probably differ among species and localities but could include variations in egg predation intensity, food availability, hatchling survival rates, or soil hydric conditions (Brown and Shine 2002, 2006b; Fitch 1970, 1982). Madagascar's geographic position in the southern tropical and subtropical zone, its latitudinal extent (12° to 25°S), and its topography produce considerable environmental variability. The climate is monsoonal, with high rainfall from December to March and dry, often cool conditions from May to September (Jury 2003). Brief observations during the dry season in the southern part of the eastern rainforests suggest that snakes are inactive, with little or no surface activity (Cadle, unpublished data). It seems likely that the strongly monsoonal climate and correlated environmental variables (e.g., soil moisture, prey abundance, and thermal conditions) probably drive the seasonal pattern of reproduction characteristic of most Malagasy reptiles.

The study of life histories of Malagasy snakes is in its infancy and the patterns of sexual dimorphism, size, and reproduction outlined in this paper provide intriguing glimpses of some unusual characteristics of this radiation. *Liopholidophis* is now among the best known Malagasy snakes but it accounts for less than 10% of the species in Madagascar and major gaps in knowledge exist even for this genus. Some highly unusual patterns of sexual dimorphism and feeding ecology are known for other Malagasy snakes (Cadle 2003) and, as shown herein, reproductive biology is sketched only in outline for a few species. Equally important, we understand little of the ecological or functional context for many observations. Thus, studies of natural history will continue to provide insight into the ecological and evolutionary significance of morphological and behavioral characteristics of these snakes. The gaps in present knowledge call for a broadly integrative approach to comprehend this radiation.

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A Revision of the New World Genus *Ceraeochrysa* (Neuroptera: Chrysopidae)

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The sixty-four known species of *Ceraeochrysa* Adams, 1982 are described, illustrated, and GEOGRAPHICAL DISTRIBUTIONS given. A preliminary phylogeny of the species is presented. Eleven species are newly described (*C. achillea, C. angusta, C. belizensis, C. bitacornua, C. chiricahuae, C. curvabilis, C. digitata, C. derospogon, C. diverticula, C. forcipata*, and *C. panamensis*). Two species are returned to this genus (*C. laufferi* and *C. placita*). Three names are synonymized: *Chrysopa silvestrina* Navás, 1929 = *Ceraeochrysa cincta* (Schneider, 1851); *Chrysopa gradata* Navás, 1913 = *Ceraeochrysa effusa* (Navás, 1911); and *Chrysopa aroguesina* Navás, 1929 = *Ceraeochrysa laufferi* (Navás, 1922). Two new lectotype designations are indicated: *Chrysopa cincta* Schneider, 1851 and *Chrysopa valida* Banks, 1895. New status is given to *Ceraeochrysa parvula* (Banks, 1903).

Ceraeochrysa Adams 1982 is a group of medium-sized green lacewings that are invariably green, often with red or brown markings laterally on the pronotum. They are commonly encountered in forest edge situations in the Neotropics and are frequently found around cultivated crops, from vegetables to orchards to field crops. As larvae they feed on many different kinds of soft-bodied insects, including eggs, caterpillars, nymphs and adults, and groups as diverse as aphids, scale insects, mealy-bugs, and lepidopterans. As such, they have the potential to be among our most important biological control agents. Already, chrysopids are released to control pests of our field crops in North America more than any other group of insects (Tauber, M.J., et al. 2000).

Ceraeochrysa is the largest genus of Chrysopini in the New World and the second largest genus (after *Leucochrysa*) of the family in that region (Brooks and Barnard 1990). Members of *Ceraeochrysa* were for many years described in the complex and variable genus *Chrysopa* and often descriptions were meager and based on slight external morphological differences that led to much proliferation of species and taxanomic confusion. Bo Tjeder (1966) was the first to recognize that structures of the male genitalia offered stable and important species differences that could help to redefine *Chrysopa* and related genera. When Phillip A. Adams described *Ceraeochrysa* in 1982, he based his definition of the genus primarily on elements of the male genitalia and he recognized 24 species and 52 synonyms. In their 1990 world generic revision of the Chrysopidae, Steven Brooks and Peter Barnard recognized 40 species of *Ceraeochrysa*. Subsequent detailed

[3] At the time of his death on 12 July 1998, Phil Adams had partially completed a manuscript to revise the genus *Ceraeochrysa*. In addition to the manuscript, he had numerous illustrations and notes on types and other specimens that he had seen during his 40+ years of study on the Chrysopidae. The manuscript, notes, and illustrations have been frequently drawn upon for this monograph and it was felt that his contribution was significant enough to include him as an author. However, many of the taxonomic decisions, especially those that pertain to the new species, are those of the first two authors.

FIGURE 1. *Ceraeochrysa smithi* (Navás, 1914): Head and prothorax, dorsal view (drawn by Marlin Peterson)

study of the chrysopid fauna of Costa Rica and Brazil has increased that number, so that John Oswald's current "Neuropterida Species of the World" on Neuroweb website contains 55 valid species of this genus. The current project recognizes 64 species, that includes 11 new ones and one resurrected name.

Ceraeochrysa is a New World genus that reaches greatest diversity and abundance in the tropics. Several species are found in warm temperate North America, and one species, *C. lineaticornis*, can be found as far north as Canada (Garland 1985; Penny et al. 1997).

Larvae of this genus are trash-bearers (Tauber, C.A., et al. 2000). That is, larvae have lateral lobes that bear long setae. Then, larvae place small objects from their environment on their backs and hold them in place with these long setae. Oftentimes, the objects are the skeletal remains of their prey. This pile of trash is thought to provide camouflage, or perhaps a buffer zone against attacking predators and parasites.

Unfortunately, to date there has never been a complete key to all species of adults, nor modern, detailed descriptions of all species. The situation is worse for larvae. There are only larval

descriptions of a few of the 14 genera of New World Chrysopini, and no definition of the genus *Ceraeochrysa* based on larval characteristics. Considering their importance in the agro-ecosystem, it has become increasingly important that this void be filled. The object of this project is to provide good keys, descriptions, and illustrations of adults so that taxonomists, field biologists, and agriculturalists have a guide that allows them to identify this major group of beneficial insects.

Also, the following species are known only from females and could not be placed effectively in the key that follows: ***C. acutipuppis***, ***C. dolichosvela, C. indicata, C. lateralis,*** and ***C. reducta***.

Material and Methods

Specimens were examined under a Wild M5A binocular microscope with 50X magnification, or an Olympus SZ60 with 63X magnification, and a Olympus CH2 compound microscope with 200X magnification, all with camera lucida attachments. Male and female genitalia were macerated in cold 10% KOH for 24 hours and stained with chlorazol Black E for 10 minutes. Genitalia were subsequently stored in glycerin in glass microvials with neoprene stoppers and placed on the pin under the specimens. For drawings of wings the wing was removed from the body and drawn with the aid of a camera lucida, and later placed on a card under the specimen with water soluble glue. Drawings of genitalia in glycerin were made with the aid of a camera lucida. Abbreviations for collections are those utilized in "Abbreviations for Insect and Spider Collections of the World" by Neal L. Evenhuis on the website hosted by the Bernice P. Bishop Museum: *<http://hbs.bishopmuseum.org/codens-inst.html>*.

AMNH – American Museum of Natural History, New York, NY, U.S.A.
BHMH – Universidade Federal de Minas Gerais, Museu de Historia Natural, Belo Horizonte, Minas Gerais, Brazil
CAS – California Academy of Sciences Collection, San Francisco, CA, U.S.A
CMT – Catherine and Maurice Tauber Collection, Davis, CA, U.S.A.
CNC – Canadian National Collection of Insects, Ottawa, Ontario, Canada
CUIC – Cornell University Insect Collection, Ithaca, NY, U.S.A.
EMUS – Utah State University Entomology Museum, Logan, UT, U.S.A.
FMNH – Field Museum of Natural History, Chicago, IL, U.S.A.
FSCA – Florida State Collection of Arthropods, Gainesville, FL, U.S.A.
INBio – Instituto Nacional de Biodiversidad, Santo Antonio de Heredia, Heredia, Costa Rica
IRSNB – Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
IZAC – Academia de Ciencias de Cuba, Instituto de Zoologia, Habana [=Havana], Cuba.
MACN – Museo Argentina de Ciencias Naturales, Buenos Aires, Argentina
MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.
MIZA – Museuo del Instituto de Zoologia Agricola, Maracay, Venezuela.
MLPA – Universidad Nacional de La Plata, Museo de la Plata, La Plata, Argentina
MNHN – Museum national de Histoire naturelle, Paris, France.
MPEG – Museu Paraense Emilio Goeldi, Belém, Pará, Brazil.
MSNG – Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy
MZBS — Museo de Zoologia, Barcelona, Spain
RBMC – R. Bruce Miller Collection, Project City, CA, U.S.A.
SEM – Snow Entomological Collection, University of Kansas, Lawrence, KS, U.S.A.
SFCC – Sergio de Freitas Collection, Jaboticabal, São Paulo, Brazil.
TAMU – Texas A. & M. University, College Station, TX, U.S.A.
UCR – University of California, Riverside, California, U.S.A.
UNAM – Universidad Nacional Autonomo de Mexico, Mexico City, Mexico.
USNM – United States National Museum of Natural History, Washington, D.C., U.S.A.

UTSTU – Utah State University Collection, Logan, UT, U.S.A.
WDS – William D. Shepard Collection, Berkeley, CA, U.S.A.
WFBM – W.F. Barr Entomological Collection, University of Idaho, Moscow, Idaho, USA.
ZMHB – Museum fur Naturkunde der Humboldt Universitat zu Berlin, Germany
ZMUH – Universität von Hamburg, Zoologisches Institut und Zoologisches Museum, Hamburg, Germany
ZMUN – University of Oslo Zoological Museum, Oslo, Norway
ZSM – Zoologische Sammlung des Bayerischen Staates, Munich, Germany

Abbreviations used in the figures

a = annals veins
af = antennal fossa
ap = apex of 7th sternite
aparc = apical plate of arcessus
arc = arcessus
apap = anterior projection of apodema
atp = anterior tentorial pit
b = copulatory bursa
cc = callus cerci
cs = chalazate setae
cu = cubital vein
dapo = dorsal apodeme
dh = dorsal hood of the gonarcus
dpa = dorsal processus of arcessus
ent = entoprocessus
ag = accessory glands
gc = gonarcus (medial arch)
gcn = gonocornua
gvp = gonocornua ventral projection
ger = gonocristae
gps = gonapsis
grc = gradate cell
gsc = gonosaccus
gst = gonosetae
ig = inner gradates
la = lateral arms of gonarcus
lg = lateral gonapophysis
lla = lateral lobe of arcessus
lparc = lateral processus of arcessus
mm = millimeters
mx = maxillary palpi
og = outer gradates
apda = anterior projection of dorsal apodeme
Psc = pseudocubitus vein
Psm = pseudomedian vein
pos = post ocular spot
Rs = radial sector
S8+9 = fused eighth and ninth sternite
Sd = spermathecal duct
Sg = spermatecal gland
T9 + ect = ninth tergite and ectoproct
v = vela
vapo = ventral apodeme
vb = ventral branch of the dorsal apodeme

Phylogeny

The strict concensus phylogenetic tree that is presented was contructed by use of the program TNT (Goloboff et al. 2000) and application of implied weights (Goloboff 1993). There was 51% symmetrical resampling. This application was utilized because of the large number of species with no males for analysis, and its function was to give less weight to homoplasies that appear in development of the tree.

The characters and states utilized were:

Character 1 – Antennal coloration (flagellum pale – 0; dark – 1)
Character 2 – Antennal scape (pale – 0; lateral stripe – 1; dorso-lateral stripe – 2; dorsomedial stripe – 3; suffused spot – 4; two stripes – 5)
Character 3 – Antennal fossa (pale – 0; small colored spot – 1; entirely colored – 2; red/black stripe – 3)
Character 4 – Postocular spot (without – 0; present – 1)
Character 5 – Frons (unmarked – 0; red/brown spot – 1; black spot -2)
Character 6 – Clypeus (unmarked – 0; laterally black – 1)
Character 7 – Gena (unmarked – 0; red colored – 1; black/brown colored – 2; red striped – 3, black striped – 4)
Character 8 – Maxillary and labial palpi (pale – 0; dark – 1)
Character 9 – Vertex (completely pale – 0; with red or black markings – 1)

Character 10 – Pronotum (without markings – 0; dark markings – 1)
Character 11 – Pronotum laterally (pale – 0; striped – 1; one spot – 2; two spots – 3; submedial spots – 4)
Character 12 – Meso- or metanotum (unmarked – 0; marked – 1)
Character 13 – Fore wing venation (transverse veins dark – 0; dark and bordered – 1)
Character 14 – Fore wings (Cubitus without veinlet – 0; with veinlet – 1
Character 15 – Fore wings (Cubitus without bordering – 0; with bordering – 1)
Character 16 – Fore wing anal veins (not bordered – 0; bordered – 1)
Character 17 – Fore wing gradate series (parallel – 0; divergent – 1; convergent – 2)
Character 18 – Fore wing gradates cell length (< m/2 – 0; >m/2 – 1; = m – 2; > m – 3)
Character 19 – Abdomen (entirely pale – 0; with dark markings – 1)
Character 20 – Male abdomen apex (normal – 0; lobed with median groove – 1; deeply grooved – 2)
Character 21 – Male abdominal apex: genital atria (lateral membrane without scales – 0; with – 1)
Character 22 – Male abdominal apex: ectoproct + 9th tergite (without ventral projection – 0; with spur – 1; with medially curved horn – 2; with large tuberculate setae – 3)
Character 23 – Male abdominal apex: dorsal apodeme of ectoproct + 9th tergite (without projection – 0; ventral projection – 1; horn-like caudal projection – 2; arrowhead-like ventral projection – 3; hook-like ventral projection – 4; projection from anterior (basal) part – 5; caudal projection as dentate plate – 6)
Character 24 – Male abdominal apex ventral projection (absent – 0; a sclerotized projection – 1; dentate – 2; a dorsal projection – 3)
Character 25 – Lateral arms of gonarcus (a vertical plate (0); a plate with dorsal projection (1))
Character 26 – Gonarcus (without dorsal plate – 0; dorsal plate pointed – 1; dorsal plate lobed – 2)
Character 27 – Gonarcus (without lateral projection – 0; with lateral projection – 1)
Character 28 – Gonocornua (without – 0; with – 1)
Character 29 – Gonocornua (tiny – 0; lobe-like – 1; horn-like – 2)
Character 30 – Gonocornua (tiny – 0; shorter than lateral arms of gonarcus – 1; longer than lateral arms of gonarcus – 2)
Character 31 – Gonocornua (tiny – 0; same plane as mediuncus – 1; elevated and straight – 2; elevated and curved – 3)
Character 32 – Gonocornua apically (tapered (0); pointed (1))
Character 33 – Gonocornua (without ventral projection – 0; with ventral projection – 1)
Character 34 – Male ninth sternite apically (normal – 0; conical – 1; bifurcate – 2)
Character 35 – Male ninth sternite apically (without tuberculate setae – 0; with – 1)
Character 36 – Male ninth sternite apically (without lateral dentate lobe – 0; with – 1)
Character 37 – Male ninth sternite (lacking cristae (0); with cristae (1))
Character 38 – Arcessus (as long as wide – 0; longer than wide – 1; very thin – 2)
Character 39 – Arcessus (without dorsal horn – 0; with two dorsal horns – 1; with lateral horns – 2)
Character 40 – Arcessus apical plate (not well defined – 0; 1- unipartite – 1; bifurcate – 2, trifurcate – 3)
Character 41 – Arcessus apical plate trifurcate (median lobe beak-like – 0; median lobe plate-like – 1)
Character 42 – Arcessus apical plate, median lobe plate-like (not flanked by lobes – 0; membranous lateral lobe not well defined – 1; branch-like lateral lobe – 2; thin lateral lobe – 3)
Character 43 – Gonapsis (absent – 0; present – 1)
Character 44 – Gonapsis (spoon-shaped – 0; not spoon-shaped – 1)
Character 45 – Gonapsis (not apically forked – 0; apically forked – 1; terminal dentate vertical plate – 2)
Character 46 – Gonapsis (without filamentous apex – 0; with apical filamentous process – 1)
Character 47 – Gonosaccus (with dispersed field of setae – 0; with two clusters of setae – 1)
Character 48 – Gonosaccus (without microteeth – 0; with field of microteeth – 1)
Character 49 – Spermatheca (pill box-shaped – 0; elongate – 1)
Character 50 – Spermatheca (short vela – 0; long vela – 1; very long vela – 2; coiled vela – 3)
Character 51 – Spermatheca shape (J-shaped – 0; U-shaped – 1; otherwise – 2)
Character 52 – Bursal gland (filamentous – 0; large, sac-like – 1; small, sac-like – 2)
Character 53 – Intramedian cell (ovate – -0, quadrangular – 1)
Character 54 – Pterostigma (pale – 0, dark – 1)

As can be seen from Fig. 2, the outgroup taxon from Leucochrysini is basal to all Chrysopini. All species of *Ceraeochrysa* came out together, and *C. placita* is seen as basal to all other species of *Ceraeochrysa*. However, results were not all satisfactory. *Chrysopodes* was seen as no more closely related to *Ceraeochrysa* than *Chrysoperla*. There were three groups of polytomies that could not be resolved and species groups did not come out together consistently, but this is understandable because so much reliance is placed on elements of the male genitalia, and in several nominate species males are unknown. Hopefully additional characters, especially at the molecular level will help resolve these problems.

Acknowledgments

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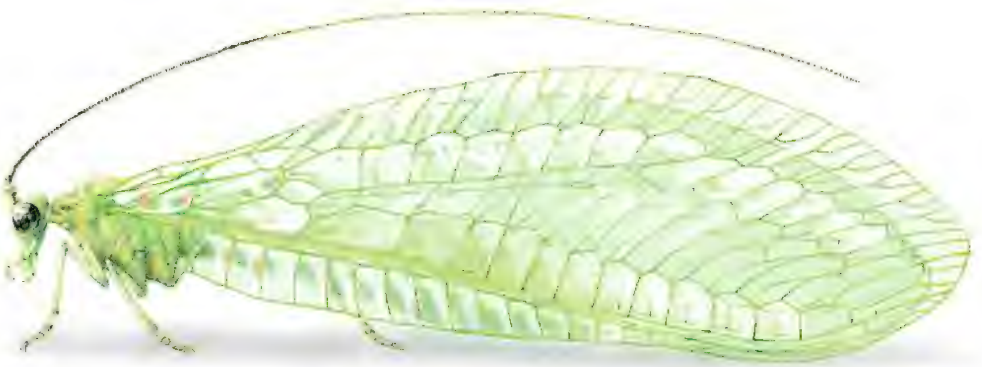
Taxonomic Treatment of the New World Genus *Ceraeochrysa*



Ceraeochrysa lineaticornis (Fitch, 1855). Habitus in lateral view (drawn by Marlin Peterson)

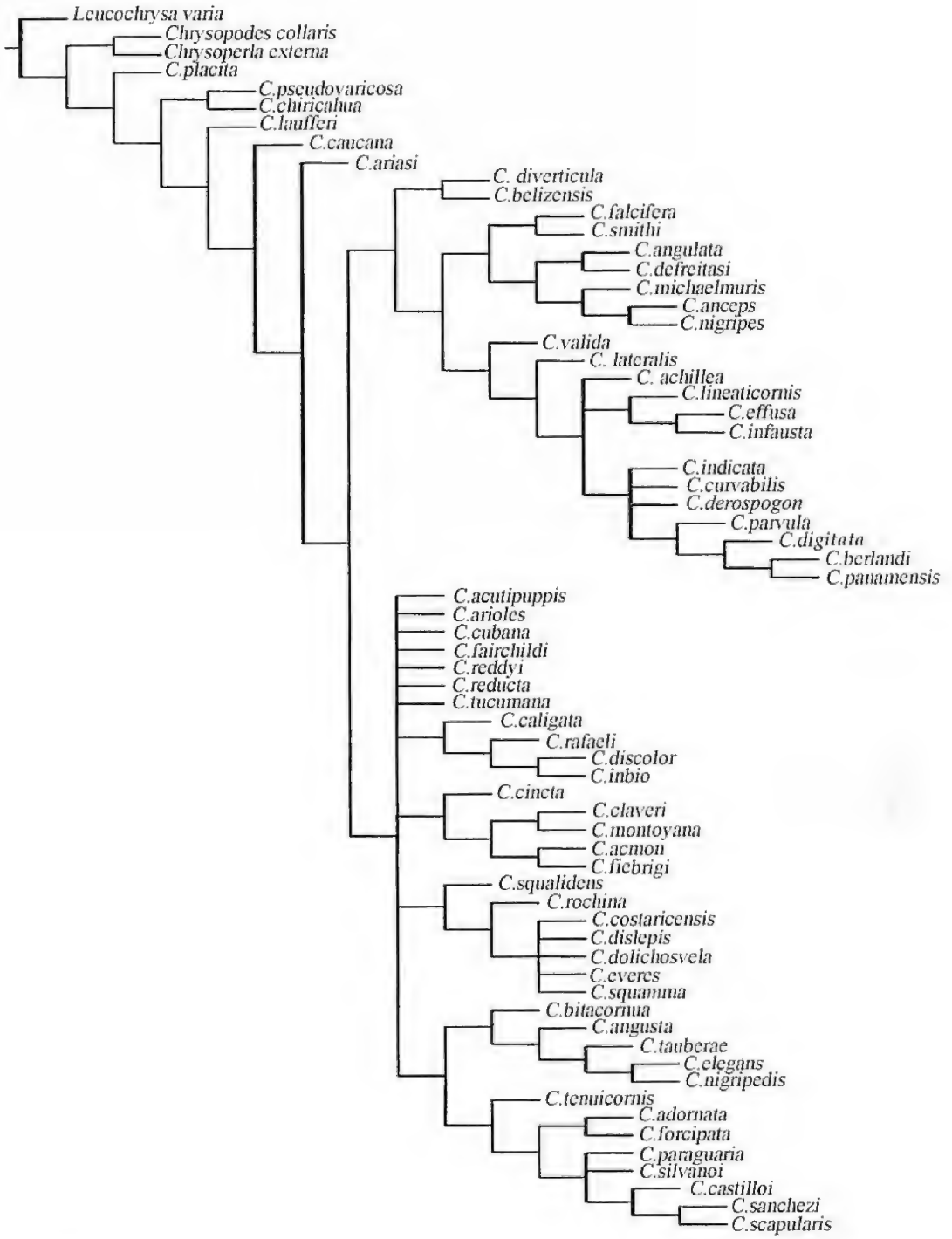


FIGURE 2. *Ceraeochrysa* genus most parcimonious phylogenetic tree.

SYSTEMATICS

Key to Species of Adult Male *Ceraeochrysa*

1. Small reticulate network of veins in middle of inner gradate series of fore wing; area of network darkly shaded ..... ***C. pseudovaricosa***
1'. Fore wing with two regular, stepwise series of gradate crossveins across apical third of wing 2
2. Pronotum with one or more pair of lateral spots, or thin, sub-medial stripes 3
2'. Pronotum with red or brown lateral stripe or no stripe 14
3. Gena, in lateral view, with two longitudinal stripes, male gonocornua closely appressed, elongate triangles 4
3'. Gena, in lateral view, with only a single longitudinal stripe, or none at all 5
4. Dark markings on head dark brown; male gonocornua extend caudally well beyond lateral arms of gonarcus ..... ***C. placita***
4'. Markings on head bright red; male gonocornua not extended caudally beyond lateral arms of gonarcus ..... ***C. chiricahuae* sp. nov.**
5. Pronotum with single pair of lateral spots 6
5'. Pronotum with two pair of lateral spots 9
6. Gradates, distal cubital cell (dcc) and crossvein 2a-3a darkly margined; lateral spots at caudal margin of pronotum; male arcessus elongate, with single tapered point 7
6'. Gradates and other crossveins not margined; lateral spots at mid-length of pronotum; male arcessus short and bifid or tripartite 8
7. Male gonocornua a simple, tapered point ..... ***C. tauberae***
7'. Male gonocornua twisted, contorted lobe ..... ***C. angusta* sp. nov.**
8. Dorsal surface of antennal scape entirely red; ventral lobe of ectoproct vertically tapered to point; male gonarcus with dorsal hood and divergent lobes before arcessus ***C. costaricensis***
8'. Dorsal surface of antennal scape with small discrete spot; ventral lobe of dorsal apodeme with recurved lobe and apical point; male gonarcus lacks dorsal hood and tiny points anterior to arcessus ..... ***C. discolor***
9. Base of dcc darkly shaded and sometimes swollen with small triangular cell at fork of CuP 10
9'. Base of dcc not shaded, swollen, nor with small triangular cell at fork of CuP 12
10. Mesoscutum with pair of dark spots; male arcessus without basal horns, with elongate, tapered, single, apical point; entoprocessus elongate, digitiform 11
10'. Mesoscutum without dark spots; male arcessus with basal pair of widely separated horns and befid apex ..... ***C. angulata***
11. Last tarsal segment of legs black; antennal scape entirely pale; abdominal tergites pale ..... ***C. nigripedis***
11'. Last tarsal segment of legs pale; lateral surface of antennal scape dark; abdominal tergites with red bands ..... ***C. elegans***
12. Pronotal spots with discrete borders; apex of male sternite VIII + IX bifurcate; two apical spiny knobs between gonapsis and sternite VIII + IX ..... ***C. paraguaria***
12'. Pronotal spots with diffuse borders; apex of male sternite VIII + IX with single apex; without spiny knobs below gonapsis 13
13. Antennal scape with dorsal stripe; gonapsis lacks lateral lobes ..... ***C. inbio***
13'. Antennal scape lacks dorsal stripe; gonapsis with lateral lobes ..... ***C. defreitasi***
14. Area of vertex behind antennal bases entirely red ..... ***C. smithi***

14'. Area of vertex behind antennal bases pale 15
15. Two red stripes on dorsal surface of antennal scape 58
15'. Dorsal surface of antennal scape entirely red, with a single dark stripe, or completely pale 16
16. Basal flagellar segments pale 17
16'. Basal flagellar segments dark 33
17. Maxillary palpi dark brown or black 18
17'. Maxillary palpi pale, or at most amber yellow 21
18. Gena entirely pale ..... *C. cubana*
18'. Gena with dark spot 19
19. Fore wing crossveins heavily margined with dark pigmentation ..... *C. panamensis* **sp. nov.**
19'. Fore wing crossveins not heavily margined with dark pigmentation 20
20. Dark stripe on lateral surface of antennal scape; fore wing with four inner gradate veins ..... *C. adornata*
20'. Antennal scape entirely pale; fore wing with seven or more inner gradate veins ..... *C. laufferi*
21. Fore wing with eight inner gradate veins; male ectoprocts 3 times as long as broad ..... *C. forcipata* **sp. nov.**
21'. Fore wing with no more than five inner gradate veins. Male ectoproct much shorter, no more than twice as long as broad 22
22. Antennal scape with stripe 23
22'. Antennal scape without stripe 28
23. Antennal scape with dorso-lateral stripe 24
23'. Antennal scape with mid-dorsal stripe 25
24. Male ventral apodeme with subapical dorsal lobe; apex of sternite VIII + IX apically rounded ..... *C. valida*
24'. Male ventral apodeme straight, without dorsal lobe; apex of sternite VIII + IX with two lateral and two medial points ..... *C. tucumana*
25. Pair of large dark red spots medially on mesoscutum ..... *C. rafaeli*
25'. Mesoscutum entirely pale 26
26. Dorsal scape stripe black; lateral pronotal stripes brown ..... *C. rochina*
26'. Dorsal scape stripe red; lateral pronotal stripes red 27
27. Ventral apodeme of male ectoproct straight and blunt-tipped ..... *C. caligata*
27'. Ventral apodeme of male ectoproct recurved and with apical point ..... *C. cincta*
28. Mesoscutum with pair of dark marks at anteriolateral margin with prescutum; male gonapsis with pair of caudal, rounded, spiny lobes ..... *C. michaelmuris*
28'. Mesoscutum entirely pale; male gonapsis lacking pair of caudal, spiny lobes 29
29. Head with dark spot along dorsal surface of gena from eyes to anterior tentorial pits; gradate veins margined with dark shading 30
29'. Head without dark marks along dorsal surface of gena; gradate veins not margined 31
30. Male gonocornua longer than two medial horns of mediuncus ..... *C. tenuicornis*
30'. Male gonocornua shorter than medial horns of mediuncus ..... *C. ariasi*
31. Fore wing crossveins all dark ..... *C. reddyi*
31'. Fore wing with most crossveins green 32
32. Male sternite VIII + IX apically deeply bilobed ..... *C. silvanoi*
32'. Male sternite VIII + IX apically rounded ..... *C. fairchildi*
33. Legs dark brown ..... *C. nigripes*
33'. Legs pale 34

34. Antennal scape unmarked 35
34'. Antennal scape with dark dorsal or dorsolateral stripe 38
35. Gena marked with red 36
35'. Gena entirely pale 37
36. Frons with pair of medial red spots; maxillary palpi pale; vertex entirely pale ..*C. caucana*
36'. Frons entirely pale; maxillary palpi amber; vertex with pair of small red spots at posterior margin ..... *C. anceps*
37. Male sternite VIII + IX with ligulate projection at laterocaudal corners that bear stout setae with conical bases; gonarcus with bilobed dorsal hood; gonapsis with dorsal double crest with appressed scales ..... *C. squalidens*
37'. Male sternite VIII + IX evenly rounded apically; gonarcus without dorsal hood; gonapsis with ventral scythe-like lobe ..... *C. falcifera*
38. Antennal scape with dorsal surface entirely darkly shaded 39
38'. Antennal scape with discrete dorsal or dorsolateral stripes 40
39. Fore wing gradate veins darkly margined; cells between gradate series 3 times longer than wide ..... *C. bitacornua* **sp. nov.**
39'. Fore wing gradate veins not darkly margined; cells between gradate series 1.5 times longer than wide ..... *C. fiebrigi*
40. Antennal scape with thin, mid-dorsal stripe 41
40'. Antennal scape with broad, dorso-lateral, dark stripe 42
41. Pronotum with broad, red, lateral stripe ..... *C. claveri*
41'. Pronotum with narrow, brown, lateral stripe ..... *C. castilloi*
42. Gena with dark markings; male gonapsis apically bifurcate 43
42'. Gena entirely pale; male gonapsis apically simple 49
43. Apex of male ectoproct rounded, with simple, thin setae 44
43'. Apex of male ectoproct pointed, with chalazae (thick-based setae) 45
44. Male gonosaccus with medial field of gonocristae; pair of caudally-directed digitiform lobes of mediuncus with another lobe ventrally; base of arcessus without pair of small dentate lobes ..... *C. parvula*
44'. Male gonosaccus lacks medial field of gonocristae; pair of dorsally-directed digitiform lobes of mediuncus without ventral lobes; base of arcessus with pair of dentate lobes ..... *C. derospogon* **sp. nov.**
45. Male dorsal apodeme of tergite IX + ectoproct with ventral branch apically extended beyond ectoproct as sclerotized, medially-directed hook ..... *C. curvabilis* **sp. nov.**
45'. Male dorsal apodeme of tergite IX + ectoproct without ventral branch apically extended; apex with only chalazae (thick-based setae) 46
46. Male ectoproct tapered caudally to a single chalazate seta ..... *C. achillea* **sp. nov.**
46'. Male ectoprocte tapered caudally to a multiple chalazate field of setae 47
47. Male sternite VIII + IX apically with fine setae; entoprocessus extremely elongate and apically bilobed ..... *C. digitata* **sp. nov.**
47'. Male sternite VIII+IX apically with chalazate setae; entoprocessus tapered to single point .48
48. Male tergite IX + ectoproct deeply divided; gonosaccus with field of gonocristae; sternite VIII + IX quadrate with one long chalazate seta at each lateral corner; ventral fork of dorsal apodeme not projected caudally beyond ectoproct ..... *C. berlandi*
48'. Male tergite IX + ectoproct not deeply divided; gonosaccus lacking field of gonocristae; sternite VIII + IX rounded with chalazate setae throughout; ventral fork of dorsal apodeme projected ventrocaudally well beyond ectoproct ..... *C. effusa*

49. Male sternite VIII + IX with upturned laterocaudal lobe; gonocornua massive, about half as wide as long and bears apical teeth ..... ***C. sanchezi***
49'. Male sternite VIII + IX gradually tapered, without laterocaudal lobe; gonocornua more slender digitiform processes with single, rounded point 50
50. Ventral fork of male dorsal apodeme projected below margin of ectoproct 51
50'. Ventral fork of male dorsal apodeme not projected below margin of ectoproct 52
51. Ventral fork of male dorsal apodeme in form of broad, anvil-shaped sclerite at ventral apex ..... ***C. acmon***
51'. Ventral fork of male dorsal apodeme in form of basal, curved hook ..... ***C. infausta***
52. Male gonarcus with dorsomedial hood arched above arcessus 53
52'. Male gonarcus without dorsomedial hood 55
53. Male dorsal hood of gonarcus evenly rounded; scales on membrane below ventral margin of ectoproct 54
53'. Male dorsal hood of gonarcus medially indented; no scales on membrane below ventral margin of ectoproct ..... ***C. dislepis***
54. Male ectoproct with ventral point; scales on membrane below ectoproct arranged on plate; gonapsis with lateral arms ..... ***C. squamma***
54'. Male ectoproct rounded ventrally; scales below ectoproct scattered on membrane; gonapsis without lateral arms ..... ***C. everes***
55. Mesoscutum with pair of dark spots at suture with premesoscutum; male sternite VIII + IX apically bifurcate; large gonocristae on membrane below gonapsis ..... ***C. scapularis***
55'. Mesoscutum entirely pale; male sternite VIII + IX apically rounded; no gonocristae on membrane below gonapsis 56
56. Male gonarcus with long lateral arms, gonarcus 3 times as long as wide ..... ***C. divaricata* sp. nov.**
56'. Male gonarcus with shorter lateral arms, gonarcus as wide or wider than long 57
57. Male gonocornua with extremely long ventral arms; dorsal projections of gonocornua widely separated at base ..... ***C. belizensis* sp. nov.**
57'. Male gonocornua with ventral extensions shorter than dorsal projections; dorsal projections of gonocornua divergent from narrow base ..... ***C. lineaticornis***
58. Basal segments of antennal flagellim dark brown to black; male unknown ..... *C. montoyana*
58'. Basal segments of antennal flagellum pale 59
59. Male abdominal sternite IX strongly recurved ..... *C. orioles*
59'. Male abdominal sternite IX bluntly truncate apically (Florida population) ..... *C. cincta*

***Ceraeochrysa acmon* Penny, 1998**

Diagnosis.— Males of this species are distinctive due to the expanded ventral tip of the ventral fork of the dorsal apodeme of the ectoproct. The often anvil-shaped form of this expansion gives this species a characteristic appearance and makes males immediately recognizable.

Head.— Vertex greenish yellow, unmarked. Frons and gena pale, unmarked. Scape straw yellow, darkened dorso-laterally; pedicel with dark stripe laterally; flagellum black. Maxillary and labial palpi pale, unmarked.

Thorax.— Green. Pronotum green with dark red stripe laterally (Fig. 3A). Meso and metathorax unmarked. **Wings**: fore wing venation mostly green, except costal crossveins 1–11, origin of Rs, R-Rs crossveins, inner and outer gradates and apex of anal veins dark. Length 14–15 mm, width 4.5–4.8 mm (Fig. 3B). Hindwing venation green, except costal crossveins and gradates dark. Hindwing length 11.5 mm: width 3.64 mm = ratio (3.16).

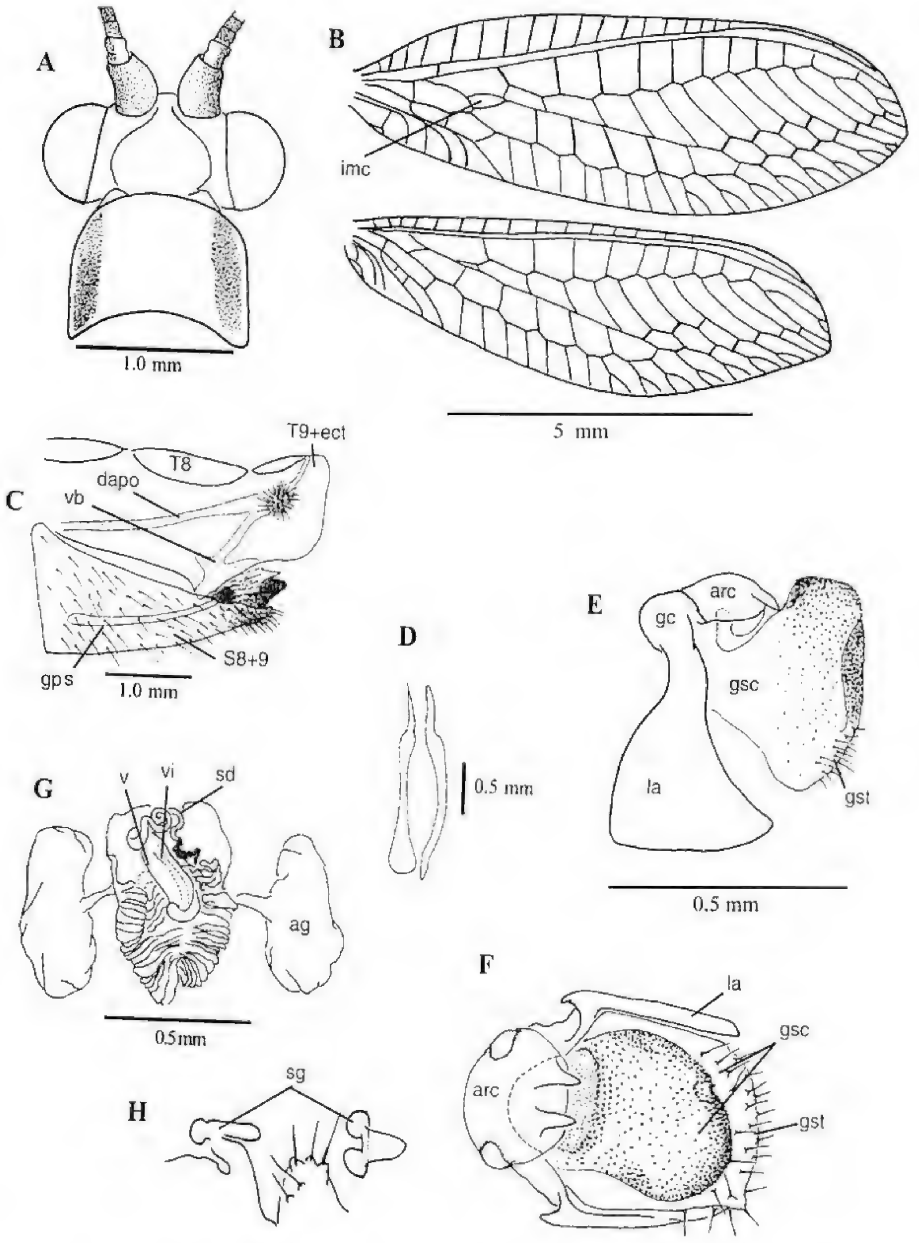


FIGURE 3. *Ceraeochrysa acmon* Penny, 1998. A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Gonapsis; E. Male genitalia, lateral view; F. Male genitalia, frontal view; G. Female genitalia; H. Subgenitale.

ABDOMEN.— Greenish yellow with small red spots on each side of tergites. **Male**: Dorsal apodeme of ectoproct with both dorsal and ventral branches widening apically (Fig. 3C). Membranous wall of genital atria juxtaposed against apex of ventral branch of dorsal apodeme with sclerotized plate of scales in several rows. Lateral arms of gonarcus long and triangular; medial arch bearing medial semicircular projections with two apical horns. Arcessus elongate, thin, caudally with tripartite apex. Gonosaccus broad, with dense field of gonocristae and long setae (Fig. 3E, F).

Gonapsis long and narrow, curved; subapically swollen; apex tapered to fine point (Fig. 3D). Apex of sternite VIII + IX with lateral projections of setae with large, tuberculate bases. **Female**: Subgenitale long, with lateral lobes and median projection (cremena) (Fig. 3H). Bursa copulatrix wrinkled with a pair of large accessory glands. Spermatheca short, J-shaped (Fig. 3G).

HOLOTYPE ♂.— **COSTA RICA: Limón**, Amubri, La Amistad Conservation Area, 9°31'40"N, 82°58'02"W, 70 m, 4–21 December 1993, G. Gallardo (INBio).

MATERIAL EXAMINED.— **COSTA RICA: Heredia,** Santo Domingo de Heredia, 12 January 2000, W.D. Shepard, (1♂)(WDS); **Limón,** Amubri, A.C. Amistad, 4–21 December 1993, G. Gallardo (1♂ – holotype)(INBio); **BRAZIL: Mato Grosso,** Corumba, 26 July 1995, S. Freitas (1♀)(SFC); Pontes e Lacerda, 14 July 1997, S. Freitas (1♂) (SFC); **São Paulo**, Jaboticabal, 20 January 1998, S. Freitas (2♀14♂)(SFC); 10 September 1997, S. Freitas (1♀)(SFC); 9 December 1995, S. Freitas (2♂)(SFC); 23 March 1995, S. Freitas (1 ♀)(SFC); **Paraná,** Foz do Iguaçu, 9–14 June 1996, M.J. and C.A. Tauber (1♂)(CMT). **BOLIVIA: Santa Cruz,** Ichilo, Buena Vista, 15 October 1963 (1♂)(CAS).

SPECIES RELATIONSHIPS.— This species appears to be part of the *cincta* group with pale gena, unmodified apical sternites, but highly modified dorsal apodeme of males. The dark antennae may align this species with *C. claveri*, but the expanded, anvil-like ventral extension of the dorsal apodeme is distinctive.

Ceraeochrysa acutipuppis Adams & Penny, 1987

DIAGNOSIS.— This species has unusual, pointed apex of the female seventh sternite with swollen-based setae. Female subgenitale is distinctly bilobed with obtusely angulate anterior margin. Externally, the unmarked head is enough to distinguish it from other related species. Male unknown.

HEAD.— Vertex green , laterally ivory. Frons pale green, genae ivory, both unmarked. Maxillary palpi pale. Scape short, green, unmarked; pedicel unmarked; flagellum pale, rather stout, with conspicuous black setation.

THORAX.— Pronotum bright green, with lateral brown stripe not reaching posterior margin; broad, width nearly twice midline length. Meso and metanotum uniformly bright green. Pleurae whitish green, with longer setae. **Wings**: Fore wing length 13.4 mm. Costal crossveins slightly fuscous: costals, basal radial , base of Rs+MA and ma-mp, gradates, cubital, ends of CuP_2, $1A_1$ and $1A_2$, 2A green. Four inner, seven outer gradates, the series parallel (Fig. 4B). Hindwing acute; four inner, seven outer gradates.

ABDOMEN.— Bright green dorsally, whitish green ventrally. Apex acute, slender (Fig. 4A). **Female**: Seventh sternite posterior margin with setal bases bearing short spines anteriorly (Fig.4C). Subgenitale short, posterior lobes domed, anterior margin angulate (Fig.4E). Copulatory bursa small, slender, bursal glands attached midlaterally. Spermatheca elongate, ends recurved; posterior end expanded rapidly, with shallow ventral invagination on ventral face (Fig. 4D); bursal duct arises from posterior margin of terminal expansion.

HOLOTYPE ♀.— **BRAZIL: Roraima**, Boa Vista, 2°44'13"N, 60°46'21"W, 10 July 1977, N.D. Penny (INPA).

MATERIAL EXAMINED.— see type.

SPECIES RELATIONSHIPS.— Wing venation and shape are similar to those of *C. cincta* and relatives. The acutely tapered abdomen, peculiar setal bases and shape of subgenitale are unique. The female's tuberculate apex of sternite VII is shared with *C. anceps*. However, the latter species has red genae, dark antennae, and the subgenitale are not so distended laterally. Until males are found and described, the relationships of this species will be in doubt.

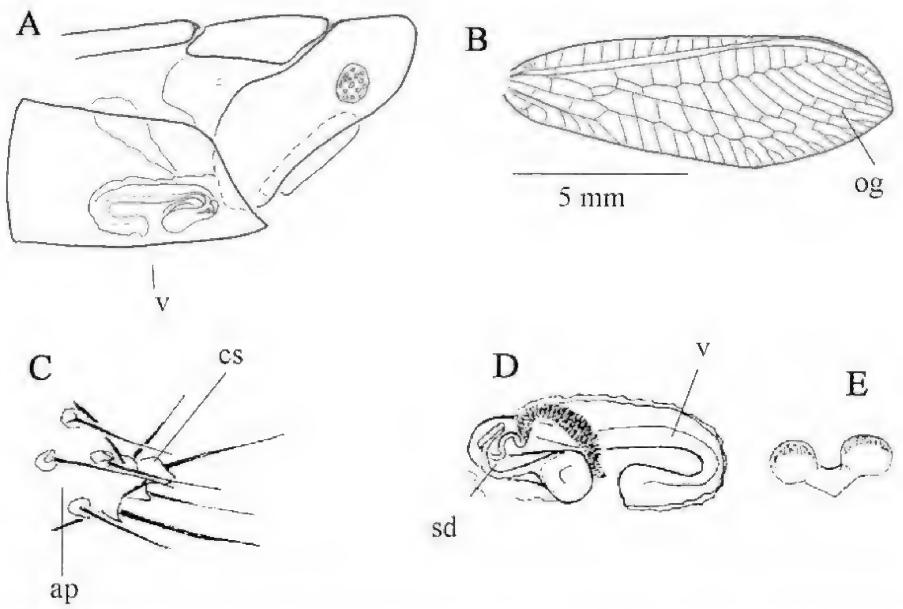


FIGURE 4. *Ceraeochrysa acutipuppis* Adams and Penny, 1987. A. Female abdomen, lateral view; B. Wing; C. 7th sternite apex; D. Spermatheca; E. Subgenitale. (Modified from Adams and Penny, 1987).

***Ceraeochrysa adornata* (Lacroix, 1926) nomen dubium**

DIAGNOSIS.— Diagnosis is uncertain due to damaged holotype. Scape with dark lateral stripe. Probably the most distinctive features are the dark palpi and red gena, but several species have these characteristics.

Description based on original description and Adams' notes of the type. Drawings were made from an Adams 1974 photograph of the type.

HEAD.— Green. Gena dark red. Maxillary palpi black. Antennal scape and pedicel with black stripe laterally; flagellum pale.

THORAX.— Pronotum green with a wide lateral red stripe; meso- and metathorax unmarked (Fig. 5A). **Wings**: Fore wing length 10 mm, first 10 costal crossveins darkly marked at intersection with Sc; other crossveins on anterior half of wing dark at ends; Rs base dark; gradates, medial crossveins and Cu_1, Cu_2, A_1, A_2 dark (Fig. 5B). Hind-wing length: 9 mm; venation pale.

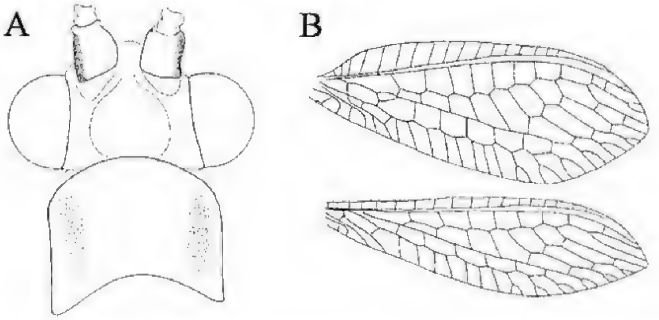


FIGURE 5. *Ceraeochrysa adornata* (**Lacroix, 1926**). A. Head and prothorax, dorsal view; B. Wings.

ABDOMEN.— missing.

HOLOTYPE.— **BRAZIL: Minas Gerais**, Uberaba, 19°45′02″S, 47°55′57″W, M. Le Moult, (1 missing abdomen)(MNHN).

SPECIES RELATIONSHIPS.— There are no distinctive features of this species to suggest species relationships. The loss of the holotype's abdomen further complicates comparisons. There are no

secondary sexually characteristics to suggest the sex of the holotype. Adams' notes suggest that this species might be *Chrysopodes* rather than *Ceraeochrysa* based on wing shape. Perhaps future advances in DNA extraction will allow molecular comparisons, but until then the relationships of this species will remain in doubt.

***Ceraeochrysa anceps* (Navás, 1926)**

DIAGNOSIS.— This species has red gena, postocular red spot, and black flagellum, which makes it quite distinctive.

HEAD.— Vertex, frons and clypeus yellow unmarked; gena red; maxillary palpi amber; postocular red spot (Fig. 6A); antennal scape and pedicel unmarked; all flagellomeres black.

THORAX.— Pronotum with red stripe laterally (Fig. 6A); pale setae; mesonotum yellow-orange. **Wings**: Fore wing costal crossveins dark posteriorly; radial crossveins dark anteriorly; gradates dark (Fig. 6B).

ABDOMEN.— **Female**: Sternite VII with tubercule at the apex (Fig. 6C); subgenitale bilobed (Fig. 6E); bursal gland sac-like (Fig. 6D); long bursal duct.

LECTOTYPE ♀.— **BRAZIL**: **Rio de Janeiro**, Nichteroy [sic], 22°52′51″S, 43°06′16″W, 26 September 1924, Kotzbauer (MNHN). Lectotype designated by LeGrand et al. (2009).

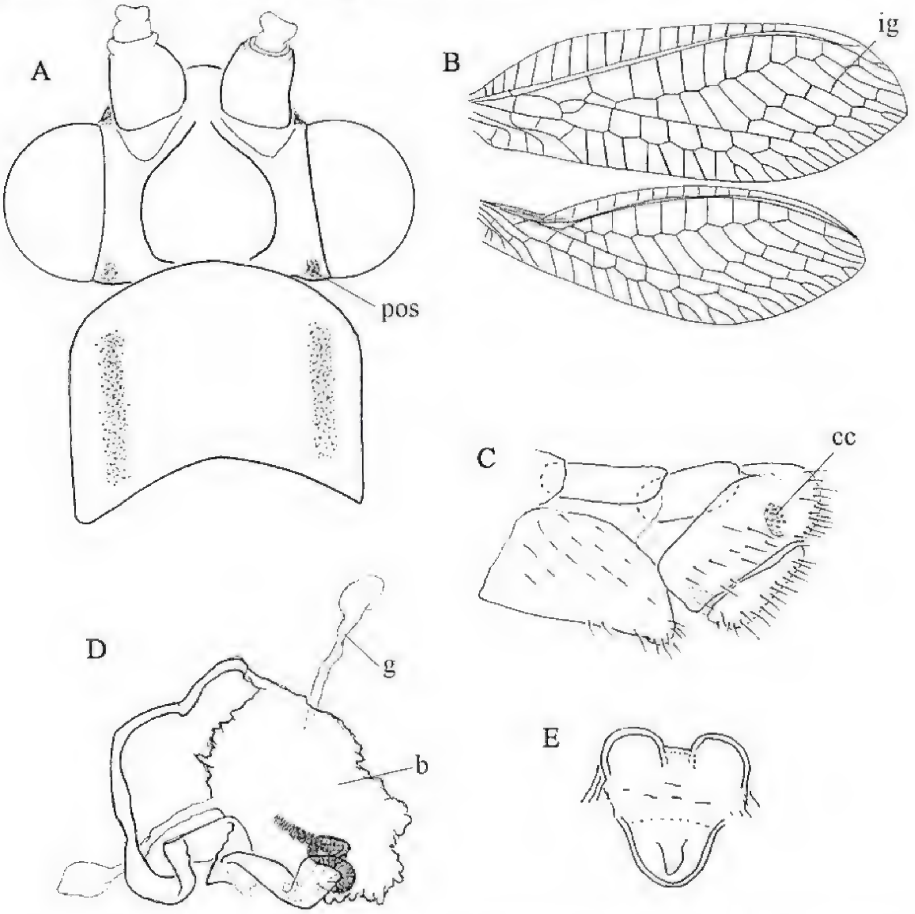


FIGURE 6. *Ceraeochrysa anceps* (Navás, 1926). A. Head and prothorax, dorsal view; B. Wings; C. Female abdomen apex; D. Female genitalia; E. Subgenitale.

SPECIES RELATIONSHIPS.— This species is similar to *C. sanchezi*, but differs in that it has red genae. This species shares with *C. acutipuppis* the tuberculate apex of the female sternite VII, but this latter species is much paler in head and antennal markings.

REMARKS.— The original description indicated that the type was in the Longinos Navás Collection, now located in the Museu de Zoologia, Barcelona, Spain. However, the type was located in the MNHN, Paris (LeGrand et al. 2009).

***Ceraeochrysa angulata* (Navás, 1929c)**

= *Chrysopa josephina* Navás, 1926 (nomen dubium)

DIAGNOSIS.— This species has an unusual thickening and dark infuscation of the membrane at the base of the distal cubital cell of the fore wing. The pronotum also has two pair of dark spots.

HEAD.— Vertex, frons, clypeus and gena unmarked; maxillary palpi pale-brownish. Antennae pedicel dark ringed; flagellum pale brown to tan.

THORAX.— Pronotum with four reddish, purplish spots at corners (Fig. 7A). Meso- and metanota pale, without markings. **Wings**: Fore wing (Fig. 7B) length 14 mm, width 5 mm; costal crossveins black; Radial, Psm-Psc; inner and outer gradates black. The most distinctive feature is a darkening of membrane surrounding the fork of the posterior cubitus and oftentimes a small basal crossvein shortly after the fork (Fig. 7B). Hindwing venation pale.

ABDOMEN.— Pale without markings. **Male**: Ectoproct dorsal apodeme with ventral branch anterior to callus cerci (Fig. 7C). Gonarcus short, very arched. Gonocornua apically forked, inferior branch longer (Fig. 7D,E). Arcessus apex forked, without lateral lobes (Fig. 7 G). Gonosaccus densely covered by gonocristae and gonosetae. Gonapsis apex thin, pointed; with short subapical lobe laterally (Fig. 7F).

LECTOTYPE ♀.— **COLOMBIA: Norte de Santander**, Pamplona, 7°22′32″N, 72°39′13″W, 1920, P. Rocheron (MNHN). Lectotype designated by LeGrand et al. (2009).

MATERIAL EXAMINED.— **COLOMBIA: Cundinamaroa,** Monterredondo, 10 January 1959, F.H. Walz (2♂♂ – CAS); 12 December 1958, F.H. Walz (1♂ – CAS); **Santander**, Pamplona, P. Rocheron, 1920 (1♀ – lectotype)(MNHN); **VENEZUELA: Aragua**, Rancho Grande, 1100 m, 11–15 January 1966, S.S. & W.D. Duckworth (1♀ – USNM); 24–31 October 1966, S.S. & W.D. Duckworth (1♂, 1♀ – USNM); 5 November 1966, S.S. & W.D. Duckworth (1♀ – USNM); 7 July 1967, R.W. Poole (1♂ – CAS); 8 August 1967, R.W. Poole (1♂ – CAS); 10–21 February 1969, Duckworth & Dietz (2♀♀ – USNM); 10 km south Rancho Grande, 14 February 1969, P. & P. Spangler (1♀ – USNM); **ECUADOR: Tungurahua,** 13 km E. Baños (1°24′S, 78°25′W), 23 January 1976, Spangler, et al. (1♀ – USNM).

SPECIES RELATIONSHIPS.— This species is part of a group of species with a swollen and darkened basal fork of the last cubital cell (often with a small cross piece) and spotted pronotum. Other members of this group include: *C. elegans, C. nigripedis*, and *C. tauberae*. These other species all have males with an elongate, tapered arcessus that ends in a single point. However, the closest relationship appears to be with *C. defreitasi*, which does not have the darkened fork of CuP. These two species share the two pair of dark spots on the pronotum; the lack of spots on the meso- and metanota; and similar male gonapses that have a small lateral lobe and thin, tapered apex.

The type female is badly discolored and has been hollowed out by psocids, but appears to have two pair of dark spots on the pronotum and no dorsal stripe on the antennal scape. LeGrand et al. (2009) report that ¾ of the antennae are also missing.

There is a series of four specimens in the Museum of Comparative Zoology from Colombia that is a part of this group of species. All have a pair of prominent dark spots at the posterolateral corner of the pronotum. The two males also have a stripe on the antennal scape, and four small dark spots on the mesonotum. The fore wings bear the typical darkening and swelling at the base of the

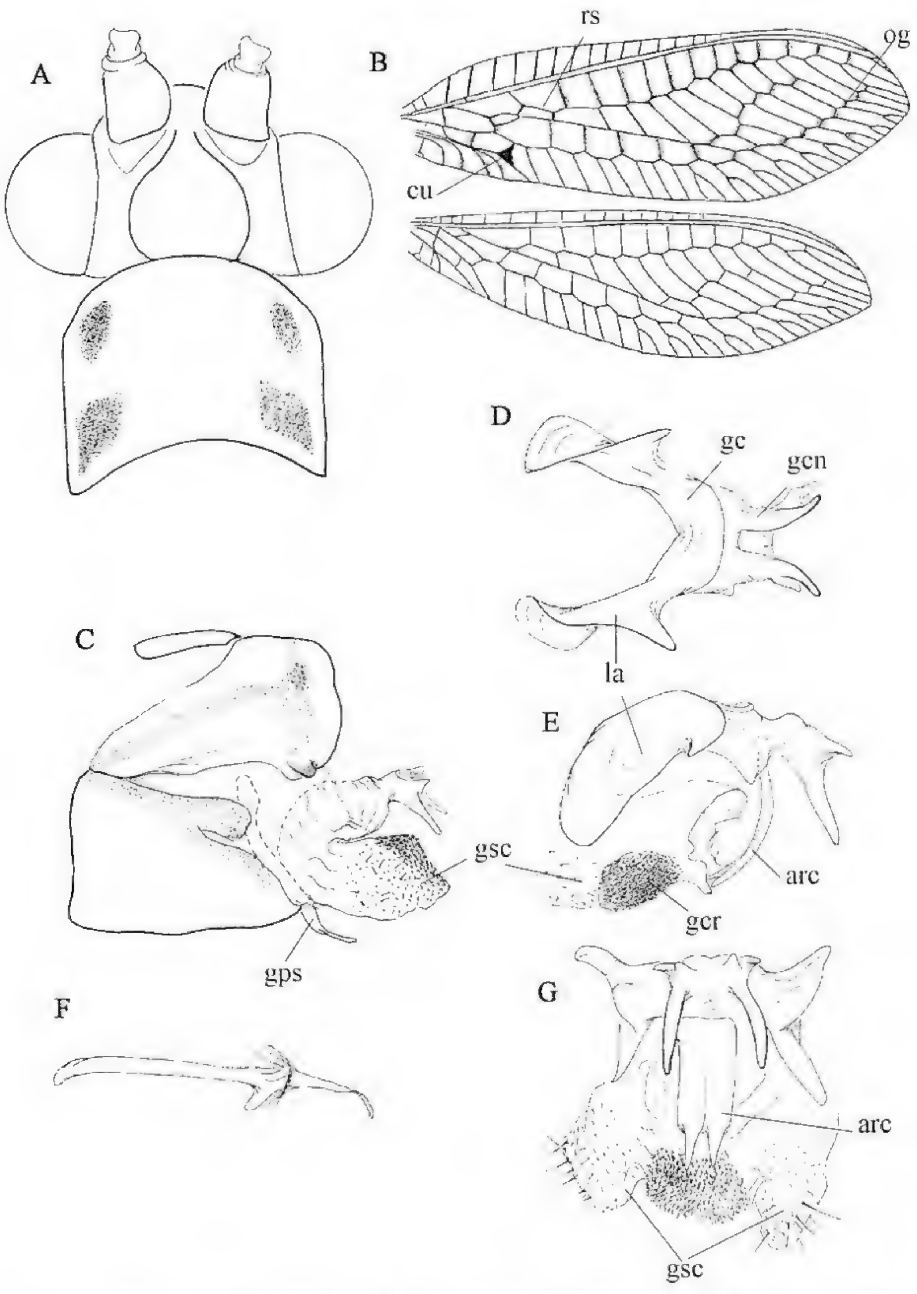


FIGURE 7. *Ceraeochrysa angulata* (Navás, 1929). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Gonapsis; G. Male genitalia, frontal view.

distal cubital cell. The two females have no such scape stripe, spots on the mesonotum, or swollen and darkened distal cubital cell. This could be a case of sexual dimorphism, or the females may belong to a different species than the males. Probably an answer to this dilemma will only be provided when the species is reared.

REMARKS.— Adams (1982) synonymized *C. josephina* with *C. angulata*. Brooks & Barnard

(1990) reversed the synonymy based on priority. The species *C. josephina* was vaguely described, with one notable characteristic, the darkened base of the distal cubital cell. However, that characteristic could fit several species, such as *C. elegans* and *C. tauberae*. The pronotum of *C. josephina* was described as marked with lateral stripes, while *C. angulata* has lateral spots. The type of *C. josephina* was purported to be in the Navás Collection, now in MZBS and could not be located, nor does it appear to be in the MNHN, Paris (LeGrand et al, 2009). With little to use to identify this species, it is probably best to consider it a *nomen dubium* closely related to the better known *C. angulata*.

***Ceraeochrysa ariasi* Adams & Penny, 1987**

DIAGNOSIS.— Small size, green overall coloration and venation with fore wing gradate series darkly bordered and dark genal marks which are distinctive for this species.

HEAD.— Vertex green, frons ivory, brown mark from eye to anterior tentorial pit (Fig. 8B); palpi pale. Antennae pale, unmarked.

THORAX.— Pronotum green with broad lateral red-brown stripe (Fig. 8A); meso- and metanota green, unmarked. Pleurae and legs pale. **Wings**: Fore wing length 10 mm; venation green, with all crossveins and many branch veins dark; inner (3) outer (5) gradates black, bordered with brown (Fig. 8B); costal area narrow.

ABDOMEN.— Unmarked. **Male**: Apodeme of tergite IX + ectoproct not distinct apically, sclerotization not extensive; no branches. Apex of sternite VIII + IX deeply cleft, no dorsocaudal processes (Fig. 8C); gonocristae small, all short, hardly longer than wide at base. Gonapsis slender, broadened caudally, shaped as in *C. tenuicornis*. Gonarcus lateral arms fairly narrow; entoprocessus narrow, vertical; gonocornua reduced, represented by a short lateral spine (Fig. 8D, E); basal horn-bearing sclerite of arcessus broad at base, horns quite long; apical arcessus sclerite tapered to slender tip, with lateral subapical barbs (Fig. 8D); gonosaccus with a single extensive field of gonosetae with rounded bases. **Female**: Sternite VII not modified; subgenitale wide, almost stalked (Fig. 8G); area anterior to subgenitale rugose, partially tanned and sclerotized; bursa small, bursal glands oval, ducts appear to open caudolaterally on bursa; spermatheca moderately elongate, arched dorsally (Fig. 8F), opening to bursa via a middorsal slit that extends its length; widened at caudal end; ventral invagination barely developed.

HOLOTYPE ♀.— **BRAZIL: Rondonia**, Vilhena, 12°44′03″S, 60°08′42″W, 7 November 1979, N.D. Penny and J.R. Arias (INPA).

MATERIAL EXAMINED.— **BRAZIL: Rondonia**, Vilhena, 7 November 1979, N.D. Penny and J.R. Arias, (1♀ – holotype)(INPA); **Amazonas**, Manaus, Am-010, Km 26, Reserva Ducke, 8 August 1978, J.R. Arias (1♂ – INPA).

SPECIES RELATIONSHIPS.— This species is similar to *C. tenuicornis* in its small size, brown genal marks, and darkly margined crossveins. These two species both have a medial plate of the mediuncus that tapers to two distal points. The two species differ in that the long, tapered gonocornua are longer than the medial plate of the mediuncus in *C. tenuicornis*. Brown genal marks are infrequently encountered in *Ceraeochrysa*; the only other Amazonian species known to have this feature is *C. everes*, which has a lateral dark scape band, and mostly pale venation, and *C. tenuicornis*.

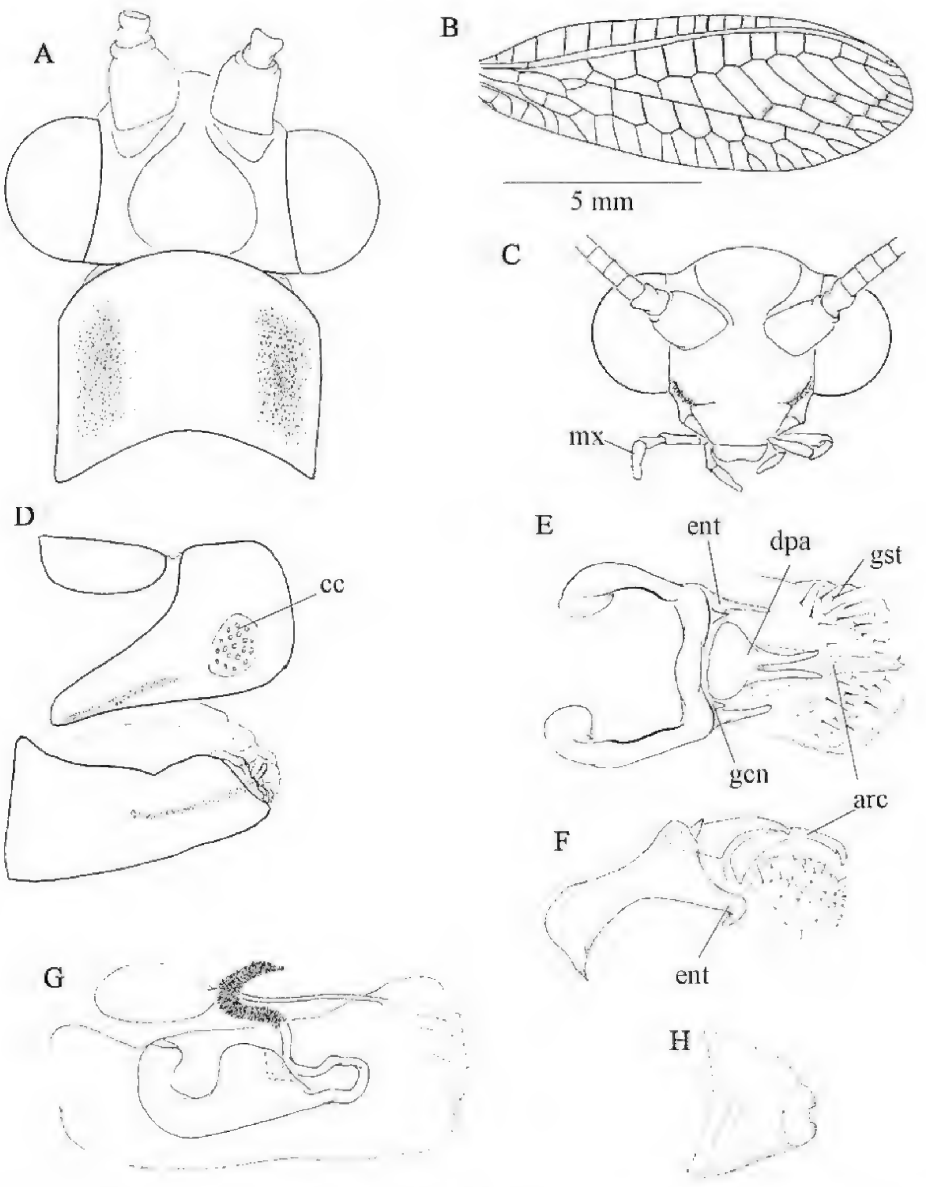


FIGURE 8. *Ceraeochrysa ariasi* Adams and Penny, 1987. A. Head and prothorax, dorsal view. B. Wing. C. Head, frontal view. D. Male abdomen apex, lateral view. E. Male genitalia, dorsal view. F. Male genitalia, lateral view. G. Female genitalia. H. Subgenitale. (Modified from Adams and Penny, 1987).

Ceraeochrysa arioles (Banks, 1944)

= *C. binaria* (Navás, 1928) [Type deposited in ZSM, destroyed] (junior homonym of C. binaría Navás, 1923)

DIAGNOSIS.— This small species has a distinctive double stripe on the dorsal surface of the scape, and males have a unique recurved apex of sternite VIII + IX.

HEAD.— Frons, clypeus, genae and labrum yellow unmarked; maxillary palpi pale; Antennal scape with two red-brown stripes, one red stripe laterally and another dorsally running through

antennal fossa to middle of vertex (Fig. 9D); pedicel laterally marked; flagellum pale, flagellomeres with black setae.

THORAX.— Pronotum green with irregular lateral pale red stripes (Fig. 9A, C); meso- and metanota unmarked. **Wings**: Fore wing length: 13 mm; and width 4 mm. Costal crossveins dark, inner and outer gradates parallel, dark (Fig. 9B); hindwing length: 11 mm; and width: 3 mm. Inner and outer gradates dark.

ABDOMEN.— Unmarked. Green. **Male**: Dorsal apodeme of tergite IX + ectoproct forked at callus cerci and with a pointed caudal process (Fig. 9E); sternite VIII + IX apically coiled upwards (Fig. 9E, H). Gonocornua very short, pointed. Arcessus as wide as long, with apical medial horn

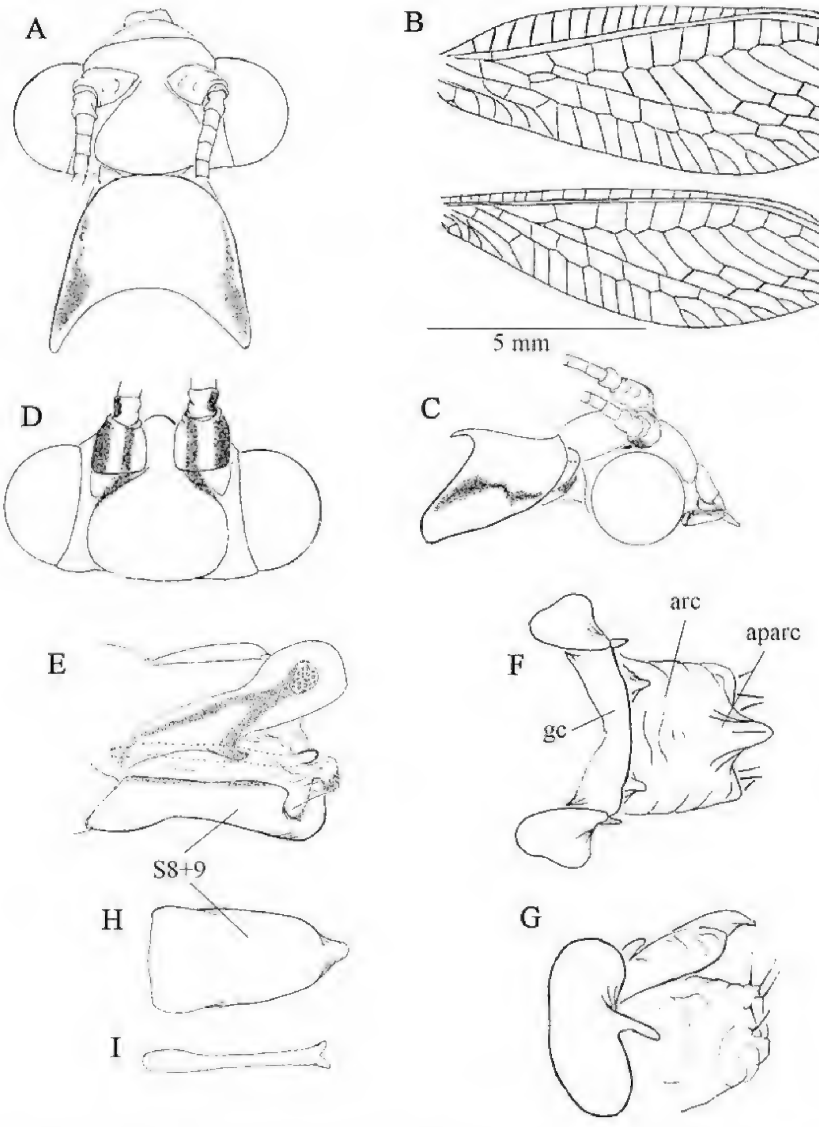


FIGURE 9. *Ceraeochrysa arioles* (Banks, 1944). A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, lateral view; D. Head, dorsal, view; E. Male abdomen apex, lateral view; F. Male genitalia, dorsal view; G. Male genitalia, lateral view; H. 8+9th sternite, ventral view; I. Gonapsis.

(Fig. 9F,G). Gonosaccus with two clusters of long gonosetae and a field of dense gonocristae. Gonapsis apically forked (Fig. 9I).

LECTOTYPE ♂.— **MEXICO: Chiapas**, Vergel, 13 May 1935, A. Dampf (MCZ). *C. binaria* Type: **COSTA RICA**: **San Jose**, San Jose, 9°55′32″N, 84°04′55″W, no date, Henry Schmidt 1 (sex undetermined)(Hamburg, destroyed). See remarks.

MATERIAL EXAMINED.— **MEXICO: Chiapas**, Vergel, 13 May 1935, A. Dampf (1♂ – lectotype)(MCZ); **Nuevo Leon**, Monte Morelos, 3 June 1931 (1♀-MCZ). **Sinaloa**, El Dorado, 22 January 1930, A. Dampf (1♂ – MCZ); **HONDURAS:** Tegucigalpa, Majica, 1 June 1959, N.D. Kraus (USNM); **COSTA RICA: San Jose,** Escazu, 17–21 January 1988, F.D. Parker (1♀ – EMUS), 7–10 April 1988 (1♂ – CAS), (1♂ – EMUS); 2–13 May 1988, (1♂ – EMUS); 3–16 July 1988, (1♀ – EMUS); 28–31 May 1989, (1♂ – EMUS); **GUYANA:** B.D. Dahlgren (1♀ – FMNH).

SPECIES RELATIONSHIPS.— This is one of the species that form the *cincta* group. Males of this group have a short, broad mediuncus with tripartite arcessus and two acutely pointed gonocornua widely separated on the gonarcus. The most distinctive feature of this group is the dorsal apodeme of tergite IX + ectoproct. In addition to the usual ventral branch that bifurcates near the callus cerci there is an additional decurved branch near the base. Three features stand out as unique in *C. arioles*: there is a double dorsal stripe on the scape; the apex of sternite 8+9 is upturned; and the basal ventral branch of the dorsal apodeme is directed anteriorly before decurved to apical point.

REMARKS.— This species was originally described as *Chrysopa binaria* Navás 1928 (a junior homonym of *Chrysopa binaria* Navás, 1923) from San Jose, Costa Rica. The type was deposited in the Hamburg Museum and subsequently destroyed during WWII. Banks (1944) recognized this homonymy and created the name *Chrysopa arioles*.

Adams (1982) chose one of Banks' type series as explicit lectotype.

***Ceraeochrysa berlandi* (Navás, 1924a)**

DIAGNOSIS.— Large species. Head, thorax and abdomen marked; ectoproct deeply divided into two lobes, with large tubercles; apex of sternite VIII + IX with large tubercles.

HEAD.— Vertex and frons golden yellow, unmarked; gena black near clypeus; clypeus laterally black (Fig. 10A,D); antennal scape black striped laterally (Fig. 10D); pedicel black ringed and with a black spot dorsally; first 19 flagellomeres black, others amber; red spot between scape and eye margin; postocular red spot.

THORAX.— Pronotum green with dark brown lateral stripe (Fig. 10C,D); meso- and metanota yellow without marks. **Wings**: Fore wing length 12 mm; width 4 mm. Longitudinal veins pale, 4–7th costal crossveins black, darkly margined; radial crossveins black, darkly margined; C-R_1 crossveins black, Psm-Psc crossveins anterior ends black and darkly margined (Fig. 10B); forked marginal veins black. Hindwing veins pale.

ABDOMEN.— Tergites marked with red (Fig.H). **Male**: Apex of ectoproct with large tubercules and deeply divided into two lobes (Fig. 10E, I). apex of sternite VIII + IX with tubercules (Fig. 10J). Gonarcus thin; lateral arms with a frontal process; gonocornua short, not parallel (Fig. 10F). Arcessus with a dorsal forked process; apical plate of arcessus with three lobes, the medial one very thin (Fig. 10F, G). Gonosaccus with a dense field of very long setae and a field of gonocristae (Fig. 10G). Gonapsis narrow, apically forked (Fig. 10K). **Female**: Spermatheca short, curved (Fig. 10L).

MATURE LARVA.— Intermandibular mark absent; epicranial mark globular, extended laterally to edge of cervical margin; lateral tubercles on abdominal segments 2–7 without marks; pronotal sclerites uncolored; venter of head without marks (Tauber & de Leon 2001).

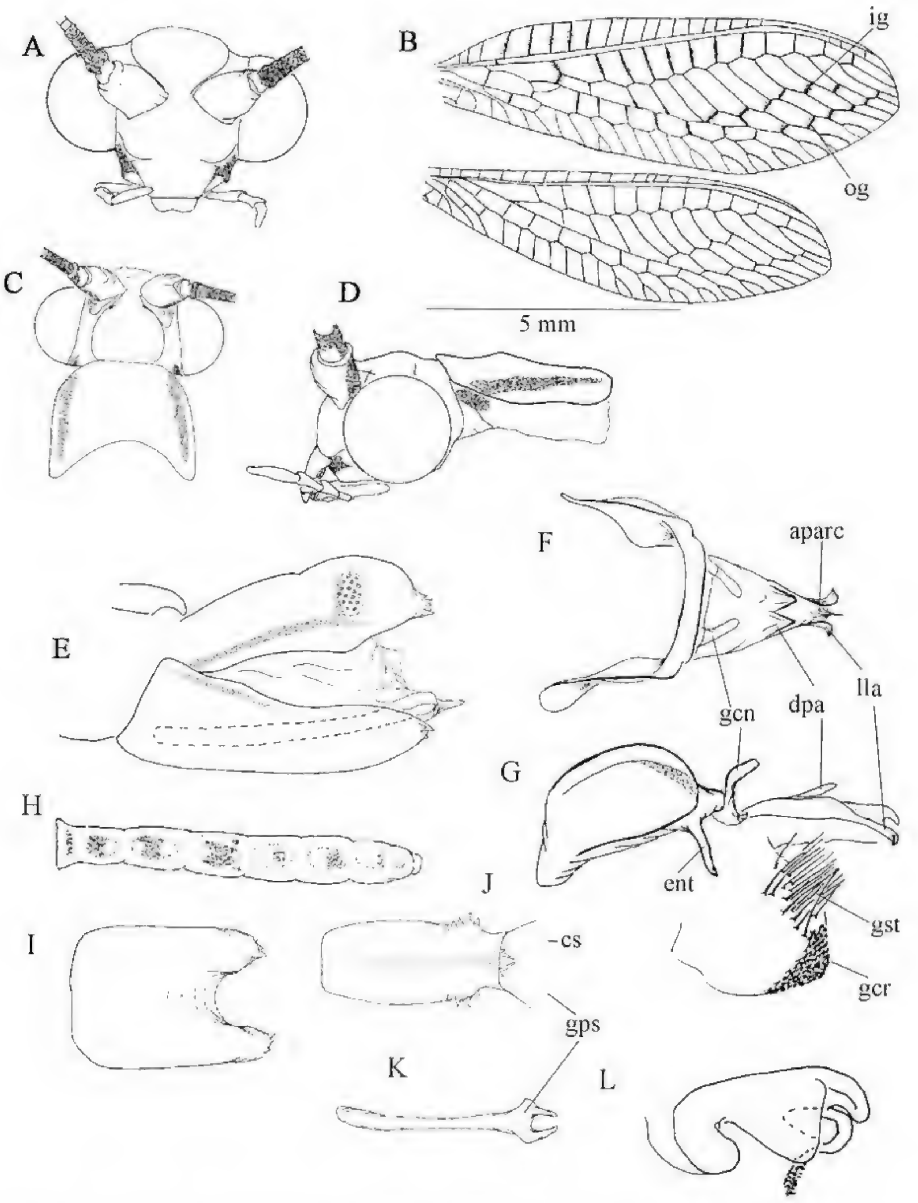


FIGURE 10. *Ceraeochrysa berlandi* (Navás, 1924a). A. Head, frontal view; B. Wings; C. Head and prothorax, dorsal view; D. Head and prothorax, lateral view; E. Male abdomen apex, lateral view; F. Male genitalia, dorsal view; G. Male genitalia, lateral view; H. Abdomen, dorsal view; I. Tergite apical, dorsal view; J. 8+9th sternites; K. Gonapsis; L. Spermatheca.

LECTOTYPE ♀.— **COSTA RICA**: (no specific locality), 1920, Paul Serre (MNHN). Lectotype designated by LeGrand et al. (2009).

MATERIAL EXAMINED.— **COSTA RICA**: 1920, Paul Serre, 1 female–type (MNHN); **Alejuela**, 8 km N Vara Blanca, 1400 m, 23 March 1992, J. McCarty & Jerry A. Powell, 1 male (UCB); **Puntarenas**, Estacion biologica Las Alturas, 12 km NE San Vito, 1550 m, 22–24 January 1993, 1 female (UCB); Osa Peninsula, Rancho Quemada, 200 m, 7-27 January 1992, A. Guitierrez, 1 ? (INBio); **Cartago**, Refúgio Nacional Fauna

Silvestre Tapantí, 1150 m, January 1992, G. Mara & F. Quesada, 1 male (INBio); **Heredia**, 16 km SSE La Virgen, 1050-1150 m, 9-21 April 2001, INBIO-OET-ALAS, 1 male (INBio).

SPECIES RELATIONSHIPS.— This is the nominate species for a group with dark antennae; very narrow, chocolate brown stripes on the pronotum; dark margining of fore wing gradate veins; and tuberculate apex of male ectoproct and sternite IX. This group appears similar to the *lineaticornis* group in many respects and might be considered a subset of that group, but can be separated by the color and width of pronotal stripes as well as the swollen bases of setae in terminal abdominal segments of males. Other members of this group include *C. infausta, C. digitata*, and *C. panamensis. Ceraeochrysa berlandi* can be separated from these other species by a lack of development on the ectoproct of the ventral process of the dorsal apodeme, and from all but *C. digitata* by the presence of a field of gonocristae ventrally on the gonosaccus.

***Ceraeochrysa caligata* (Banks, 1946)**

DIAGNOSIS.— Antennal flagellum pale; scape with one dorsal stripe. Pronotum with red lateral stripe. Fore wing gradate series long, parallel, unshaded. Male dorsal apodeme with long ventral branch, basally attached; arcessus as broad as long; gonapsis a simple rod.

HEAD.— Green; frons and gena pale without marks. Scape and pedicel with thin dark red stripe continued onto membranous base (Fig. 11A); flagellum pale. Maxillary palpi pale.

THORAX.— Green; pronotum with dark red stripe laterally (Fig. 11A), mesonotum with dark marks; metanotum unmarked. **Wings**: Venation green with some transverse veins black or darkened. Fore wing: costal crossveins 4 to 10, origin of Rs, R-Rs crossveins 1 to 2, 4 to 8, inner and outer gradates, Psm-Psc crossveins 3 to 5 black. Length 15 mm, width 6 mm (Fig. 11B). Hindwing length 14 mm, width 4 mm.

ABDOMEN.— Green, unmarked. **Male**: Ventral arm of dorsal apodeme of tergite IX + ectoproct apically blunt and upturned (Fig. 11C). Gonarcus narrow, curved. Gonocornua long and decurved (Fig. 11E, F). Arcessus broad, with a pair of lateral and subapical horns, apically decurved. Gonosaccus with sparse elongate setae. Gonapsis thick and short (Fig. 11G). **Female**: Subgenitale short and thick, forming part of a heavily sclerotized plate (Fig. 11H); bursa large sac-like; spermatheca with short ventral impression.

MATURE LARVA.— Intermandibular mark present; postfrontal marks absent; prothoracic sclerites uncolored (Tauber & de Leon 2001).

HOLOTYPE ♂.— **PANAMA:** Puerto Cabello, 11 June 1908, Englehart. (MCZ).

MATERIAL EXAMINED.— **PANAMA:** Puerto Cabello, 11 June 1908, Englehart. (1♂-holotype)(MCZ); **BRAZIL: Amazonas:** Manaus, 25 September 1976, (1♂- INPA); 6 November1976, N.D. Penny, (1♂- INPA); **Mato Grosso**: Itiquira, 13 January 1997, S. Freitas (1♂1♀-SFC); **Pará:** Belém, Utinga, 16 January 1980 M. F. Torres, (1♂- MPEG); Oriximiná, Rio Trombetas, M. Branco, 19 November 1982, José Binda and João Vidal (1♂1♀ – INPA). **São Paulo**: Jaboticabal, 24 October 1990, A.D. Silva, (1♂- SFC); 2 September 1993, R. Narciso, (2♀♀)(SFC); January 1995, C.H.J. Scomparin (1♂- SFC); Taquaritinga 16 October 1993, A.L.Q. Xavier (1♂ – SFC).

SPECIES RELATIONSHIPS.— This species is a member of the *cincta* group of species with a recurved ventral projection of the male dorsal apodeme of the ectoproct. The pale antennae separate *C. caligata* from *C. claveri* and *C. scapularis*. *Ceraeochrysa caligata* is probably most similar to *C. cincta*, but males can be separated by the longer, more slender ventral projection of the dorsal apodeme and longer gonocornua of *C. caligata*.

This species is not distinguishable from *Ceraeochrysa cincta* on non-genitalic characters. The female genitalia differ only slightly: the spermatheca is more elongate in *C. caligata*, and the lip of the subgenitale more prominent. These differences are not sufficiently distinctive to be useful in

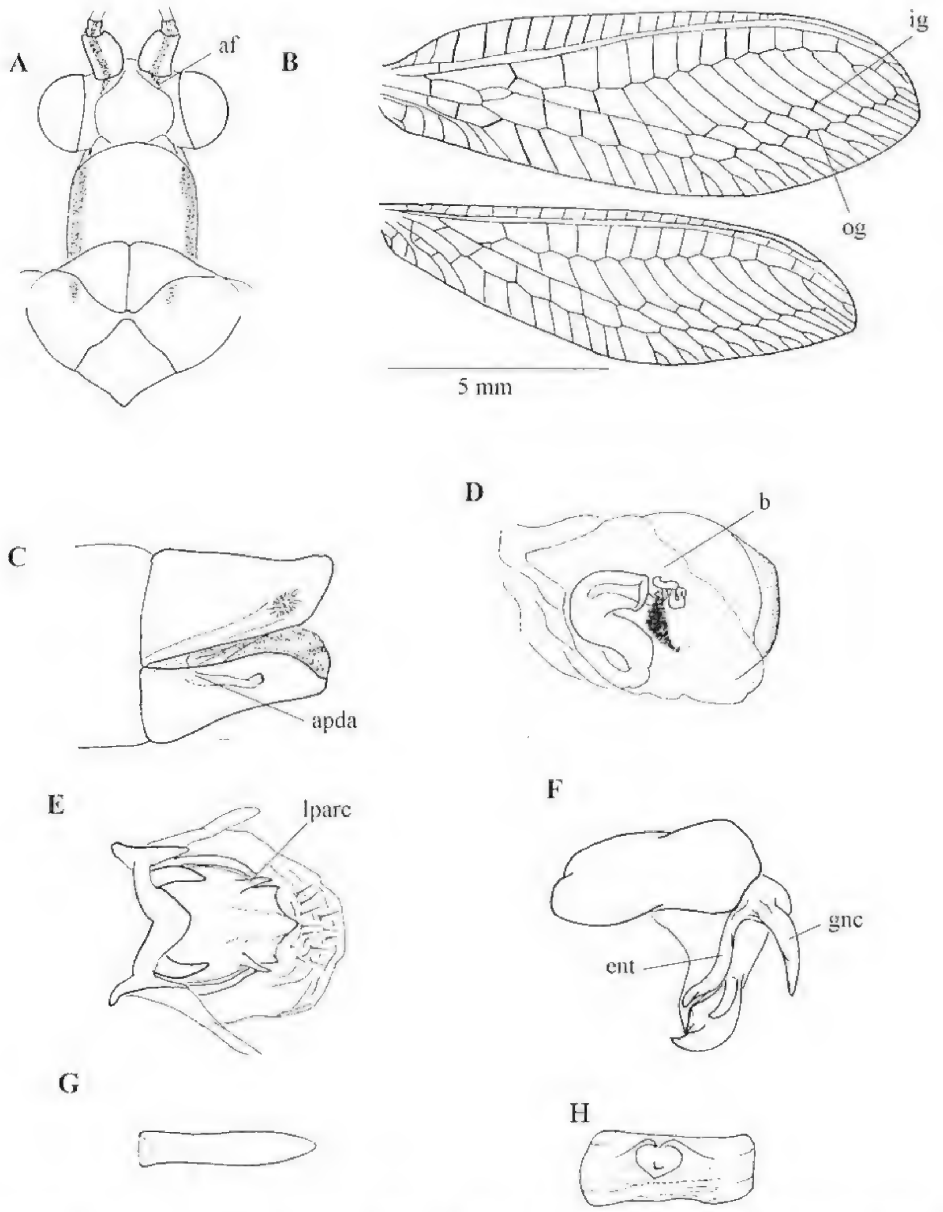


FIGURE 11. *Ceraeochrysa caligata* (Banks, 1946). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Female genitalia; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Gonapsis; H. Subgenitale

identification. The male genitalia are quite similar, differing in the shape of the ventral projection of the ninth tergite apodeme, which is curved for its entire length with apical point in most *C. cincta*, and straight with blunt apex in *C. caligata*. The gonocornua of *C. caligata* are relatively longer (5X width), while those of *C. cincta* are shorter (2X width).

REMARKS.— We have not been able to locate the type locality "Puerto Cabello" in Panama. There is a well-known locality by this name in Venezuela (10°28′08″N, 68°00′39″W), and this may be the type locality.

LeGrand et al. (2009) took *C. cornuta* out of synonymy with *C. cincta* and resurrected its status as a valid species based on unspecified characters of the female type. They also synonymized *C. caligata* with *C. cornuta,* again without specifying the basis for this synonymy. We have found that females of *C. cincta* and *C. caligata* cannot be separated with any degree of reliability, and hereby place *C. cornuta* back into synonymy with *C. cincta* and resurrect *C. caligata* as a valid name.

***Ceraeochrysa castilloi* (Navás, 1913a)**

DIAGNOSIS.— Specimens with black antennal flagellum and a lateral stripe on the scape.

HEAD.— Light yellow, vertex pale, frons, clypeus and gena pale; antennal scape with a lateral black stripe (Fig. 12B); flagellum all black.

THORAX.— Pronotum with very narrow light red stripe (Fig. 12A); meso and metanotum unmarked. **Wings**: Fore wing length 14 mm, width 5 mm; costal crossveins dark brown; radial and medial crossveins dark; base of Rs dark; cubital crossveins dark; gradates inner and outer dark (Fig. 12C). hindwing: slightly dark costals and sectorials.

ABDOMEN.— **Female**: Spermatheca short, vela right turned (Fig. 12D, E); subgenitale well sclerotized (Fig. 12F).

HOLOTYPE ♀.— Label without locality, 3 April, Blatt (ZSM). The original publication by Navás indicates type is from Paraguay: San Bernardino.

MATERIAL EXAMINED.— **BRAZIL:** (MCZ); **Rio de Janeiro**, Rio de Janeiro, 2 May 1870, B.P. Mann (1?- MCZ); **PARAGUAY: Cordillera,** San Bernardino, 25°15′37″S, 57°14′35″W, 3 April, Blatt (1♀- holotype)(ZSM).

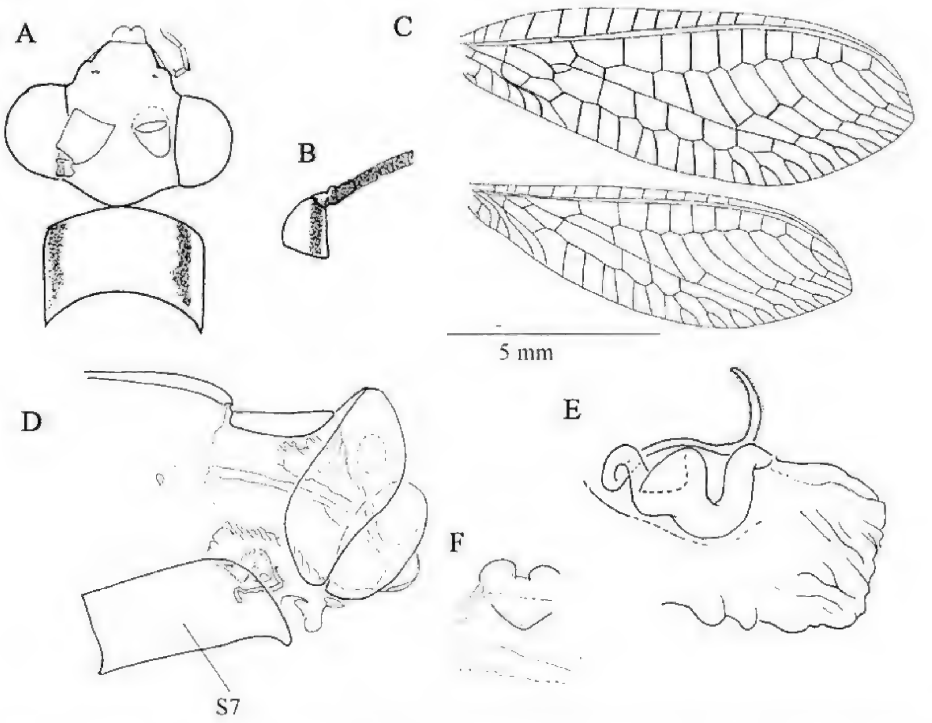


FIGURE 12. *Ceraeochrysa castilloi* (Navás, 1913a). A. Head and prothorax, dorsal view; B. Antennal base; C. Wings; D. Female abdomen, apex; E. Spermatheca; F. Subgenitale.

SPECIES RELATIONSHIPS.— In the key this species comes out together with *C. claveri*. However, *C. claveri* is a member of the *cincta* group with reddish coloration, whereas *C. castilloi* appears to be part of the *lineaticornis* group with dark brown coloration. The male of this species is still unknown and its species relationships are unclear.

Ceraeochrysa caucana (Banks, 1910)

DIAGNOSIS.— This species has yellowish or greenish body, a faint reddish mark under each eye on the frons; antennal flagellum black basally, pale apically; a red stripe laterally on pronotum. Fore wing costal area unusually broad basally with crossveins black; gradates and most transverse veins dark,

HEAD.— Pale or greenish; frons with two faint red spots (Fig. 13C); clypeus unmarked; gena red; antennal scape pale, unmarked; flagellum black becoming pale apically.

THORAX.— Pronotum with lateral red stripes near margins (Fig. 13A); meso and metanota unmarked. **Wings**: fore wing length 15 mm, costal area wider than usual; costal crossveins black; gradate series, inner (6) outer (7), black, crossveins connecting radial sector to radius, black in the middle (Fig. 13B); other transverse veins dark.

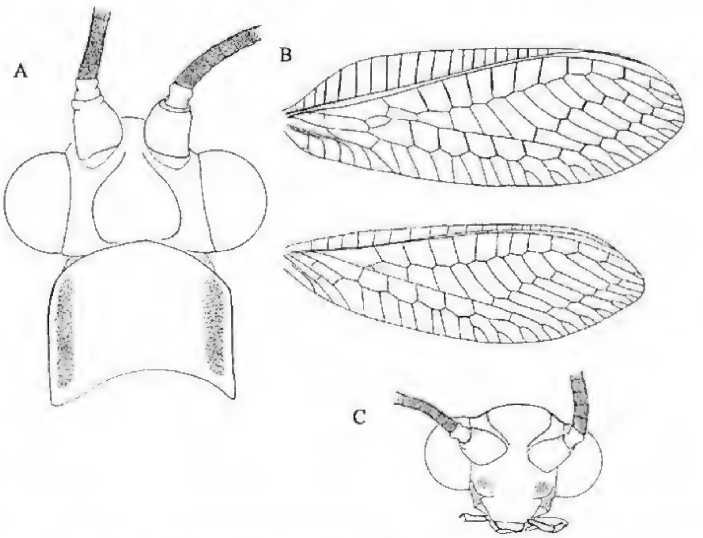


FIGURE 13. *Ceraeochrysa caucana* (Banks, 1910). A. Head and thorax, dorsal view; B. Wings; C. Head, front view.

ABDOMEN.— not dissected.

HOLOTYPE ♀.— **COLOMBIA: Cauca**, Inmba, 1000 m, January, Fassl (MCZ).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Colombia, Brazil

SPECIES RELATIONSHIPS.— This species may be a *Chrysopodes*. The red marks below the eye on the frons and broad basal costal area of the fore wing are frequently found associated with species of *Chrysopodes* (*Chrysopodes*). Without a male the affinities of this species remain in doubt.

Ceraeochrysa cincta (Schneider, 1851)

Chrysopa cincta Schneider, 1851 (Brazil, lectotype (no abdomen), ZMHB, teneral) **new designation**
Chrysopa bilineata Navás, 1914a (Guatemala, type ♀ in BMNH)
Chrysopa bruchi Navás, 1914b (Argentina, lectotype ♂)
Chrysopa lafonei Navás, 1914b (Argentina, type ♂ in MNHN, teneral)
Chrysopa incalis Banks, 1915 (Peru, type ♂ in MCZ)
Chrysopa thallina Navás, 1919 (Argentina, type ♂ in MLPA)
Chrysopa bicarnea Banks, 1920 (USA, type ♂ in MCZ, teneral)
Chrysopa advena Navás, 1922b (Uruguay, lectotype ♂ in MNHN)
Chrysopa habana Navás, 1922b (Cuba, type not found)
Chrysopa bessona Navás, 1924b (Argentina, type ♀ in MLPA)

Chrysopa mestiza Navás, 1924c (Cuba, type ♀ in MCZ)
Citameva bina Navás, 1924c (Cuba, Type ♂ in MCZ)
Chrysopa villosula Navás, 1924d (Cuba, type in MCZ, no abdomen)
Chrysopa cornuta Navás, 1925a (Brasil, type ♀ in MNHN)
Chrysopa silvestrina Navás, 1929b (Paraguay, type in MSNG) **new synonymy**
Chrysopa alternans Navás, 1933b (Peru, type ♂ in ZMHB, teneral)
Chrysopa wollebaeki Esben-Petersen, 1934 (Galapagos, 6♂♂, 1♀ syntype series in ZMUN)
Chrysopa iona Banks, 1944 (Surinam, type ♂ in MCZ)
Chrysopodes sallei Banks, 1946 (Mexico, type ♂ in MCZ)

DIAGNOSIS.— Antennal flagellum pale; scape and pedicel with single, dorsal stripe. Pronotum with broad, red, lateral stripe. Fore wing gradate series long, parallel, unshaded. Male dorsal apodeme of ectoproct with recurved ventral branch basally attached. Arcessus broad, gonocornua widely separated, only about twice as long as wide. Gonapsis a single, unforked rod.

There is a population of this species in Florida with a double dorsal scape stripe.

HEAD.— Vertex green; gena and frons pale yellow, unmarked; maxillary palpi pale; antenna pale, apex fuscous; scape and pedicel with dorsal dark red stripe (Fig. 14A).

THORAX.— Green; pronotum with dark red stripe laterally (Fig. 14A); meso- and metanota unmarked. **Wings**: Fore wing venation mostly yellowish green, except costal crossveins 5–11, origin of Rs, R-Rs crossveins 1–4, inner and outer gradates, Psm-Psc crossveins 1–4, and endings of anal veins dark (Fig. 14B). Length 14 mm width 5 mm. Hindwing costal crossveins, R-Rs crossveins, and middle part of Rs black. Length 11 mm; width 3.6 mm.

ABDOMEN.— Green, unmarked. **Male**: Dorsal apodeme of tergite IX + ectoproct heavily sclerotized with a posteriorly-directed ventral branch (Fig. 14C). Gonarcus with vertically flattened lateral arms and two caudally-directed, medial horns (gonocornua)(Fig. 14H, I). Entoprocessus elongate, extended well below arcessus. Arcessus with a transverse basal plate with two latero-apical horns; and apical sclerite with a decurved apical point. A field of tiny gonocristae arranged in rows above sternite VIII + IX. Gonapsis long, slender, apically upturned (Fig. 14F). **Female**: Area between subgenitale and sternite IX heavily sclerotized (Fig. 14D). Subgenitale with ventral invagination that lacks central projection (Fig. 14G). Spermatheca U-shaped, short (Fig. 14E), linked to bursa by a short duct; bursa wrinkled, sac-like.

LECTOTYPE (without abdomen).— **BRAZIL: Rio de Janeiro,** Rio de Janeiro, N. Thom. (ZMHB).

MATERIAL EXAMINED.— **U.S.A.: Florida**, Highlands Co., Archbold Biological Station, 3 June 1966, R.G. Beard (2♀♀ – TAMU); 5 June 1966, R.G. Beard (1♂ – TAMU); 6 June 1966, R.G. Beard (3♀♀ – TAMU); 12 June 1966, R.G. Beard (2♀♀ – TAMU); 13 June 1966, R.G. Beard (1♀ – TAMU); 15 June 1966, R.G. Beard (1♂, 1♀ – TAMU); 25 June 1966 R.G. Beard (1♀ – TAMU); 27 March 1967, R.G. Beard (1♀ – TAMU); 28 March 1967, R.G. Beard (1♀ – TAMU); Highlands Hammock State Park, 28 Dec. 1965, R.G. Beard (1♂ – TAMU; Manatee Co., Bradenton, 4 Sept. 1958, E.G. MacLeod (2♀, 1?–TAMU); Marion Co., Weirsdale, 20 Nov. 2958, M. Muma (1♂, 1♀ – TAMU); Miami-Dade Co., Miami, July 1922, G.F.Moznette (♂-type of *C. bicarnea*)(MCZ); 4 July 1949, E.G. MacLeod (1♂ – TAMU); Paradise Key, Everglades Nat. Park, 29 March 1952, J. R. Volkeroth (♀-CNC); Pinellas Co, 3 mi S. Largo, 12 September 1957, E.G. MacLeod (♂-TAMU); Indian Rock Beach, 11 Sept. 1957, E.G. MacLeod (2♀ – TAMU); Largo, 11 Sept. 1957, E.G. MacLeod (2♀ – TAMU); 13 July 1962, E.G. MacLeod (1♀ – TAMU); Palm Harbor, 16 Sept. 1958, M. Muma (1♂, 3♀ – TAMU); 13 May 1959, M. Muma (2♂♂ – TAMU); 11 June 1959, M. Muma (1♂, 3♀♀-TAMU); Allen's Grove, 13 Nov. 1958, M. Muma (1♂, 3♀♀ – TAMU); 12 Feb. 1959, M. Muma (1♂, 1♀ – TAMU); Polk Co., Lake Alfred, June 1956, M. Muma (1♂, 1?–TAMU); 19?? (♀- CAS); Grovecoll (1♂ – TAMU); **MEXICO: Oaxaca**, 2–3 mi S Matias Romero, 22 April 1962, F. Parker and L.A. Stange (♂-FSCA); (no exact locality nor date), Salle (♂-type of *C. sallei*)(MCZ); **GUATEMALA: Sololá,** V. [volcano] de Atitlan, 2500–3500 ft. [762–1066 m], Champion (1♀-type of *C. bilineata*)(BMNH); **HONDURAS: Cortés**, San Pedro Sula, 3 August 1973, P. Adams, (2♀-CAS); **CUBA**: **Matanzas**, Cienaga de Zapata, March 1964, I. Gar-

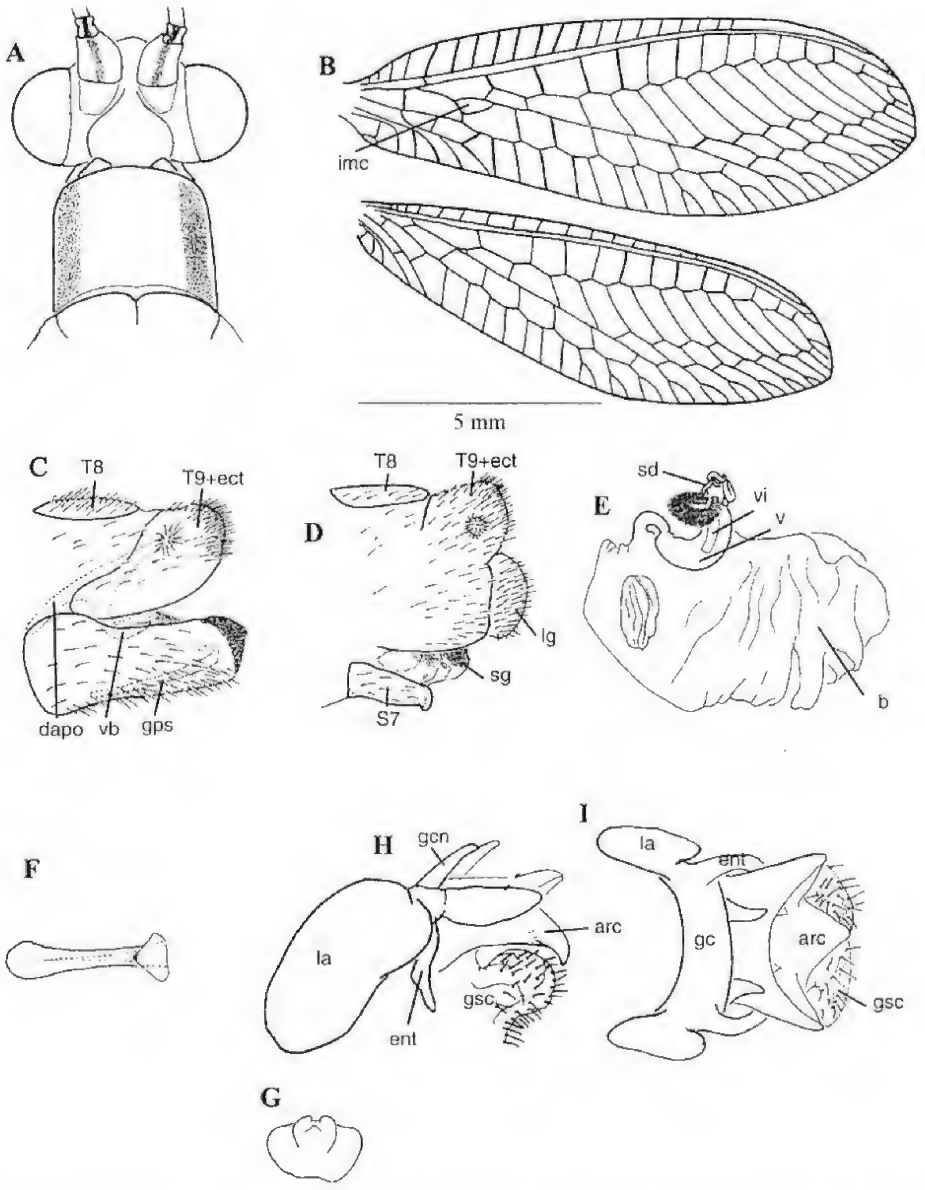


FIGURE 14. *Ceraeochrysa cincta* (Schneider, 1851). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Female abdomen apex, lateral view; E. Female genitalia; F. Gonapsis; G. Subgenitale; H. Male genitalia, lateral view; I. Male genitalia, dorsal view.

cia (1♂ – TAMU); **Oriente**, Santiago, Mar Verde, June 1964, P. Alayo (1♂ – TAMU); Habana [Havana], Rio Almendares, 3 August 1922, F. Cervera (♂-type of *C. cubana* var. *mesonota*)(MCZ); Rio Almendares. 19 July 1923, F. Cervera (♀ type of *C. mestiza*)(MCZ); Santiago de las Vegas (Havana), 4 December 1923, F. Cervera (1 without abdomen – type of *C. villosula*)(MCZ); **JAMAICA:** Frome Estate, Aug. 1959, F.D. Bennett (1♂ – TAMU); **PUERTO RICO:** Rio Piedras, 9 March 1913, J. R. Johnston (♂-USNM); **SURINAM: Paramaribo**, Paramaribo, 3 December 1938, Geijskes, (♂-syntype of *C. iona*)(MCZ); **ECUADOR: Galapagos Islands,** Narborough Island, 28 March 1899, R.E. Snodgrass (♂- USNM); **PERU: Lima**, Lima, 4 October 1932, (♂- type of *C. alternans*)(ZMHB); 30 August, Parish, (1♂- MCZ); Matucana, 7788 ft. [2373 m],

14 June, Parish (♂- syntype of *C. incalis*)(MCZ); **Piura**, Chosica, 2800 ft. [853 m], 10 June, Parish (1?-syntype of *C. incalis*)(MCZ); **BRAZIL: Rio de Janeiro**, Rio de Janeiro, 1? – lectotype of *C. cincta*)(ZMHB); Nictheroy [sic], 25 November 1924, (♀-type of *C. cornuta*)(MNHN), **São Paulo**: Taquaritinga, 5 March 1994, 1 (sex unknown), A.L. Xavier (3♂♂-SFC). **PARAGUAY: Guairá,** Villa Rica [Villarica], December, F. Schade (MCZ); **URUGUAY**, coastal region, 1920, D. Renato Martin (♂-type of *C. advena*)(MNHN). **ARGENTINA: Buenos Aires**, La Plata, 28 November 1920, C. Bruch (♀-type of *C. bessona*)(MLPA); 13 March, C. Bruch (♂- type of *C. lafonei*)(MNHN); **Catamarca**, Huasán, 25 February 1912, C. Bruch (♂-lectotype of *C. bruchi*)(MACN); (1♂-paratype of *C. bruchi*)(MZBS); (2♀♀- paratypes of *C. bruchi*)(MLPA); Catamarca, C.S. Reed. (♂-type of *C. thallina*)(MLPA); La Risueña, November 1925 (1♂-MZBS).

GEOGRAPHICAL DISTRIBUTION.— Schneider described this species from Brazil. It has been recorded (under various names) from the following countries: southern U.S.A., Cuba, Jamaica, Puerto Rico, Mexico, Guatemala, Honduras, Costa Rica, Panama, Ecuador (Galapagos Is.), Guyana, Surinam, Brazil, Peru, Uruguay, Paraguay, and Argentina.

INTRASPECIFIC VARIATION.— Coloration of this species is extremely variable over its extensive range. The scape can bear a single longitudinal line, two longitudinal lines, or a single subapical spot. The flagellum may be either pale or black but is pale in most South American specimens, dark in most Florida specimens. Pronotal markings can vary from the normal two longitudinal, lateral lines to three dark spots in Peruvian specimens, to two lateral spots in Bolivian and Uruguayan specimens. However, throughout the range, the male genital remain consistently the same.

SPECIES RELATIONSHIPS.— This species is the nominate member of the group of species with a recurved ventral projection of the dorsal apodeme of the ectoproct. It can be separated from *C. montoyana, C. scapularis* and *C. claveri* by the presence in these species of dark antennae. Additionally, *C. scapularis* has dark spots on the mesonotum, *C. montoyana* has a double scape stripe and *C. claveri* has an apically bifurcate gonapsis. Though closely related, *C. caligata* males have a longer, thinner ventral projection of the dorsal apodeme of the ectoproct and longer gonocornua.

REMARKS.— The species *C. silvestina* was described for a specimen from Villarica, Paraguay with an unusual pair of dark marks in the middle of the pronotum. Although we have not seen the type specimen, there is a series of specimens from the same locality in the MCZ. Some of the specimens have the pair of dark spots and others do not. The dark spots appear to be obvious muscle scars and the series appears to otherwise be normal *C. cincta*. Thus, the two names are herein synonymized. Earlier synonymies are those of Adams, 1982 and Adams and Penny, 1987.

The original description of *C. cincta* mentions specimens in the ZMHB and Selys-Longchamps Collection (now in IRSNB). There has apparently never been a lectotype designated. Three specimens of this series exist in the ZMHB. One of these specimens bears a green label that reads "cincta Schn, Rio 04, N. Thom. Ber." It is somewhat teneral and now is missing the abdomen. This specimen appears to be the presumed type and we will follow common usage by explicit designation as the lectotype.

The type of *Chrysopa lafonei* was supposedly in the Navás Collection, but was located in the Paris Museum.

Ceraeochrysa claveri (Navás, 1911)

Chrysopa claveri Navás, 1911 (Colombia, lectotype ♂ in MNHN)
Chrysopa silvana Navás, 1913a (Brazil, type in unknown location)
Chrysopa deficiens Navás, 1930 (Argentina, type ♂ in MZBS)
Citameva sibirica Navás, 1930 (Argentina, type ♀ in MZBS)
Chrysopa haitiensis Smith, 1931 (Haiti, type ♂ in MCZ)
Chrysopa adoina Banks, 1946 (Mexico, type ♂ in USNM, teneral)
Chrysopa inexpectata Alayo, 1968 (Cuba, type ♂ in IZAC)

DIAGNOSIS.— This species is often more yellow in coloration than others of the genus. It is a member of the group of species with males that have a recurved ventral projection of the dorsal apodeme of the ectoproct. This is one of the species which has black antennae, but it has dark-red stripes on pedicel and scape that continues to vertex membranous area. The male genitalia has a forked gonapsis as its most distinctive characteristic.

HEAD.— Vertex golden yellow; frons and gena pale, unmarked; pedicel and scape with a dorsal mid-line continued onto antennal basal membrane as a triangular spot (Fig. 15A); flagellum black; maxillary and labial palpi pale.

THORAX.— Green; pronotum yellow with dark red stripe laterally (Fig. 15A); meso- and

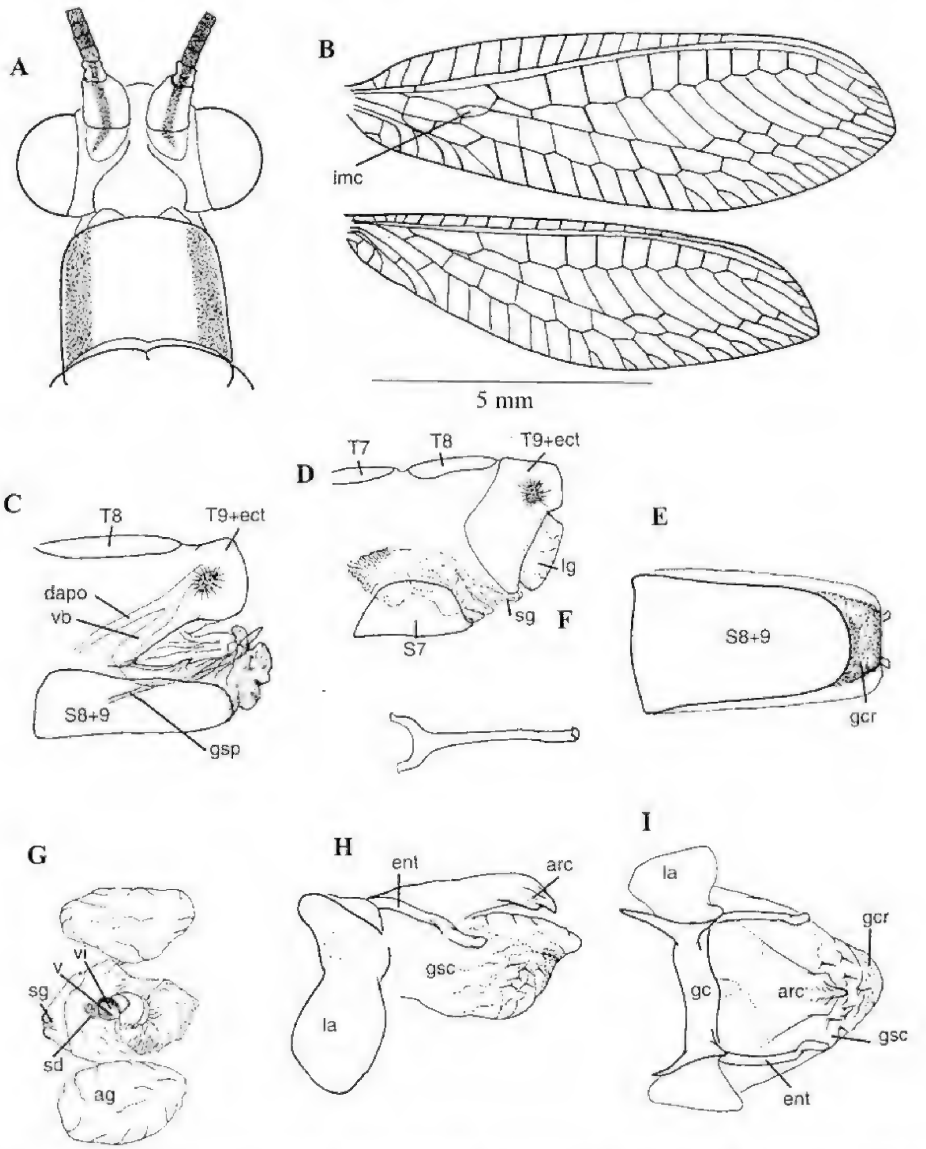


FIGURE 15. *Ceraeochrysa claveri* (Navás, 1911). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Female abdomen apex, lateral view; E. Male abdomen apex, ventral view; F. Gonapsis; G. Female genitalia; H. Male genitalia, lateral view; I. Male genitalia, dorsal view.

metanota unmarked. **Wings**: Venation mostly green with some crossveins black; fore wing costal crossveins 4–12, origin of Rs base, R-Rs crossveins, Rs-Psm crossveins 1–4, gradates, Psm-Psc crossveins 6–8, unforked marginal veins, and cubital and anal vein apices dark (Fig. 15B). Length 14 mm, width 5 mm. Hindwing costal crossveins 5–13, R-Rs crossveins, and gradates dark. Length 14 mm, width 4 mm.

ABDOMEN.— Green, unmarked. **Male**: Dorsal apodeme of tergite IX + ectoproct bearing ventral fork which is apically acute (Fig. 15C). Gonapsis long, slender posteriorly forked (Fig. 15F). Gonarcus not arched (Fig. 15I). Entoprocessus long, caudally pointed (Fig. 15H). Arcessus short, membranous, triangular in dorsal view, without dorsal horns (Fig. 15I). Gonosaccus with sparce gonosetae; above apex of sternite VIII + IX a field of gonocristae (Fig. 15E). **Female**: Area between subgenitale and sternite VII heavily sclerotized (Fig. 15D). Bursa copulatrix with a pair of large glands (Fig. 15G). Spermatheca elongate, U-shaped, ventral impression elongate.

MATURE LARVA.— Intermandibular mark present; frontal marks distinct; frontal mark oblong; prothorax with three large sclerites and five to six pairs of small secondary sclerites; lateral tubercles on abdominal segments II-VI marked with brown (Tauber & de Leon 2001).

LECTOTYPE ♂.— **COLOMBIA:** without specific locality, 1840, C. Parzudaki (MNHN). Lectotype designated by ADAMS (1982).

MATERIAL EXAMINED.— **MEXICO:** (1♂-holotype of *C. adoina* taken at quarantine in New Orleans on 4 February 1936) (USNM); **HAITI:** Pentionville, 22 December 1928; Port-au-Prince, 8 February 1929, R.C. Smith (♂- paratype of *C. haitiensis*)(MCZ); 19 February 1929 (♀ – paratype of *C. haitiensis*)(MCZ); **HONDURAS:** (1♀-paratype of *C. adoina* taken at quarantine at Charleston, SC on 25 June 1936(MCZ); **COLOMBIA:** (no locality), 1840, C. Parzudaki, 1840 (♂- lectotype of *C. claveri*)(MNHN); **FRENCH GUIANA:** St. Jean du Maroni, April-May 1914, R. Benoist.(1♂-type of *C. incalis*)(MNHN); **BRAZIL: Amazonas:** Manaus, 25 September 1976 to 8 March 1977, N.D. Penny (5♂♂, 7♀♀-INPA). **Ceara**: Maranguape, W. M. Mann (1? – MCZ); **Bahia**, 1913, P. Serre (1♂-MNHN); **Mato Grosso:** Itiquira, 7 September 1999 (3♂♂4♀♀-SFC). **São Paulo:** Taquaritinga, 16 October 1993, (2♂♂, 3♀♀-SFC); 5 March 1994, A.L.Q. Xavier, (2♂♂, 2♀♀-SFC); 7 January 1993, S. Freitas (2♂♂-SFC); **ARGENTINA**: **Jujuy**, Siberia, 1929, Brisout (♂-type of *C. deficiens*)(MZBS).

GEOGRAPHICAL DISTRIBUTION.— Mexico, Cuba, Haiti, Guatemala, Panama, Honduras, Puerto Rico, Colombia, Guiana, Surinam, Trinidad, Brazil, Argentina.

SPECIES RELATIONSHIPS.— Of the known species of the *cincta* group, this is the only one with dark antennae. The male genitalia are similar to others of the group, except that it has no visible gonocornua on the gonarcus.

REMARKS.— The original type series in the Paris Museum was from Colombia and Panama (Navás 1911) and consisted of four specimens (R.C. Smith notes). Navás had indicated in the original description that this was a "espèce colombienne." There are now two specimens in this series from Colombia with four identical labels "1) Museum Paris/Colombie/C. Parzudaki 1846, 2) green disc, 3) Chrysopa/claveri/Nav., 4) Chrysopa/haitiensis/ ♂ Smith/compared with type/det. E. MacLeod '68". One of the specimens now has no abdomen. The other specimen was designated lectotype by Adams (1982).

The species *Cintameva sibirica* was originally described in an article on Asian Neuroptera, the author apparently misinterpreting the locality Siberia in northwestern Argentina for the better known region of Russia.

Ceraeochrysa costaricensis Penny, 1997

DIAGNOSIS.— This species has pale green to yellow features, except for a pair of dark spots in the middle of the pronotum and no dark marks on the meso- and metanota.

HEAD.— Vertex, frons, clypeus, gena and palpi bright yellow. Antennal scape with orange suffused dorsally, pale yellow ventrally (Fig. 16A); pedicel and flagellum pale yellow.

THORAX.— Pronotum wider than long, pale green with pair of large reddish brown spots laterally (Fig. 16A). Smaller red brown spot under antero-lateral margins on either side of pronotum. Meso- and metanota pale green. **Wings**: Fore wing length 13.5 mm; longitudinal veins pale; crossveins dark, except for apical costal crossveins (Fig. 16B). Hindwing length 12.0 mm, venation pale; with three inner and seven outer gradate veins.

ABDOMEN.— **Male**: Tergite IX + ectoproct elongate, with scattered chalazate setae; an acute posteroventral lobe supported by ventral lobe of dorsal apodeme (Fig. 16C); sternite VIII + IX tapered to apex with chalazate setae. Gonarcus narrow medially, with narrow pair of elongate, upturned lateral arms, which end in dorso-caudal acute point (Fig. 16D, E). Arcessus with pair of small projections basally and an evenly decurved medial point apico-ventrally; convoluted field of small gonocristae on gonosaccus. Gonapsis relatively short, with subapical lateral arms and acute, upturned apical point.

HOLOTYPE ♂.— **COSTA RICA: Puntarenas**, Las Alturas, 8°56′19″N, 82°58′02″W, 1360 m, 27 February 1991, Helen Sparrow (INBio).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Costa Rica.

SPECIES RELATIONSHIPS.— The male genitalia has a dorsal hood on the gonarcus which indicates a close relationship with *C. everes*, but the latter species has longitudinal red stripes laterally on the both sides of the pronotum.

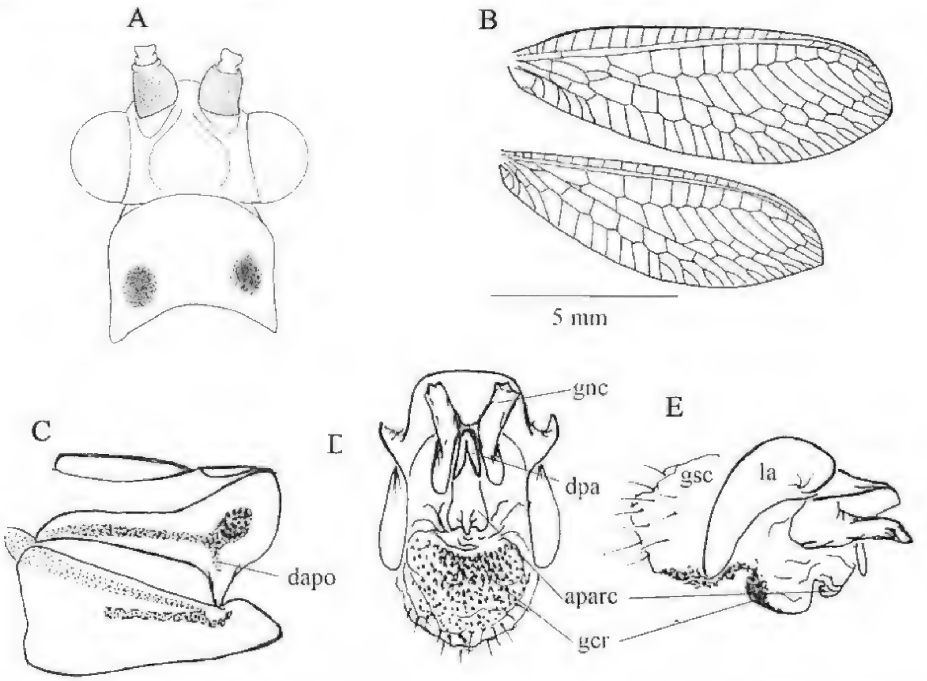


FIGURE 16. *Ceraeochrysa costaricensis* Penny, 1997. A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Male genitalia, frontal view; E. Male genitalia, lateral view.

***Ceraeochrysa cubana* (Hagen, 1861)**

Chrysopa cubana Hagen, 1861 (Cuba, neotype ♂ in MCZ)
Chrysopa tolteca Banks, 1901 (Mexico, type ♀ in MCZ)
Chrysopa albatala Banks, 1913 (Surinam, type [without abdomen] in MCZ)
Chrysopa venularis Navás 1913b (Jamaica, type ♀ in ZSM)
Chrysopa imbecilla Navás, 1914a (Barbados, type ♂ in BMNH)
Chrysopa seminole Banks, 1924 (USA, type ♀ in MCZ)
Chrysopa epheba Navás, 1924c (Cuba, type not found) (Alayo, 1968)
Chrysopa freemani Smith, 1931 (Haiti, type ♂ in MCZ)
Chrysopa fischerina Navás, 1933a (Brazil, type ♀ in MBHU)
Chrysopa damiensis jamaicensis Banks, 1941 (Jamaica, type ♀ in MCZ)

DIAGNOSIS.— The combination of short pronotum with broad stripes, dark-tipped palpi, dark crossveins, and single vein from third medial cell to wing margin quickly distinguishes this species group. Females are indistinguishable from the more northern *C. valida*. Males have a number of autapomorphies: abdominal spiracles are quite enlarged; the apical arms of sternite VIII + IX are bifurcate, spiny, and conspicuous; there are several large gonocristae on the gonosaccus; and the gonarcus has a vertical dorso-medial plate. Males also have a rugose vertex which is otherwise only found in *C. paraguaria*, *C. scapularis,* and *C. valida*.

HEAD.— Green; vertex glossy on females and rugose on male (Penny and Freitas 2001), unmarked; scape with a thin dark red stripe dorso-laterally (Fig. 17A); flagellum pale; frons and gena unmarked. Apical two segments of maxillary palpi dark.

THORAX.— Green. Pronotum with pale red stripes laterally; meso- and metanota unmarked. **Wings**: venation green with black crossveins: fore wing costal crossveins 2–15, origin of Rs, R-Rs crossveins 1–8, inner and outer gradates, Pms-Psc crossveins 3–8, and cubital and anal veins apices dark (Fig. 17B). Length 11 mm, width 4 mm. Hindwing costal crossveins 4–12, R-Rs veins 1–4 and inner and outer gradates dark; length 11 mm, width 3 mm.

ABDOMEN.— Green unmarked. **Male**: Dorsal surface of tergite IX + ectoproct deeply cleft; apex of sternite VIII + IX with pair of lateral forcipate projections (Fig. 17C,D); dorso-laterally to ninth sternite two lobes that bear teeth and setae (Fig. 17C). Gonarcus broad with a dorso-medial, plate-like lobe (Fig. 17G). Entoprocessus short. Arcessus apico-medially decurved and acute. Gonosaccus with long setae (Fig. 17F). Gonapsis long and wide. **Female**: Spermatheca short. Bursa sac-like, wrinkled (Fig. 17E)

MATURE LARVA.— Intermandibular mark absent; epicranial mark globular, extended laterally to edge of cervical margin; lateral tubercles on abdominal segments II-VII marked with brown; frontal marks narrow, separate; genal mark not entended ventrally; distal segment of labial palpi cream to pale brown; pronotal plates (T1–Sc1) with small clear area interiorly.

NEOTYPE ♂.— **CUBA:** Soledad, near Cienfuegos, 6–20 August, N. Banks (MCZ).

MATERIAL EXAMINED.— **U.S.A.: Florida**, Alachua Co., Gainesville, 2 Sept. 1959, A. Vazquez (2♂♂, 3♀♀ – TAMU); Bay Co., Panama City Beach, 19 July 1995, J.D. Oswald and L.A. Stange (5♀♀ – TAMU); Brevard Co., Cape Canaveral, Artesia, 22 Dec. 1948, H.L. Chamberlain (1♂, 1♀ – TAMU); Titusville, 22 Aug. 1950, W.F. Chamberlain (1♀ – TAMU); Broward Co., Fort Lauderdale, 4 June 1930, M. Bates (1?-MCZ); 8 July 1933 (1?-MCZ); 16 June 1933 (1?-MCZ); 23 June 1933 (1?-MCZ); 25 June 1933 (1?-MCZ); 7 July 1933 (1?-MCZ); Collier Co., Marco, 24 July, Mott (♀- type of *C. seminole*)(MCZ); Highlands Co., Sebring, 5 November 1956 (1♀-MCZ); 16 October, C.T. Parsons (1?-MCZ); 27 October (1?-MCZ); November 1942 (1?-MCZ); Indian River Co., Sebastian, April, G. Nelson (1?-MCZ); Miami-Dade Co., Everglades National Park, Long Pine Key, 1 December 1961 Munroe, Glen, Holland & Chilcott (1♂, teneral-CNC); North Miami Beach, 4 April 1967, P. Liles (1♂ – TAMU); Monroe Co., Big Pine Key, 1 July, M. Bates (1?-MCZ); Orange Co., Winter Park, 21 March, C.H. Paige (1?-MCZ); 9 November, E.M. Davis (1?-MCZ);

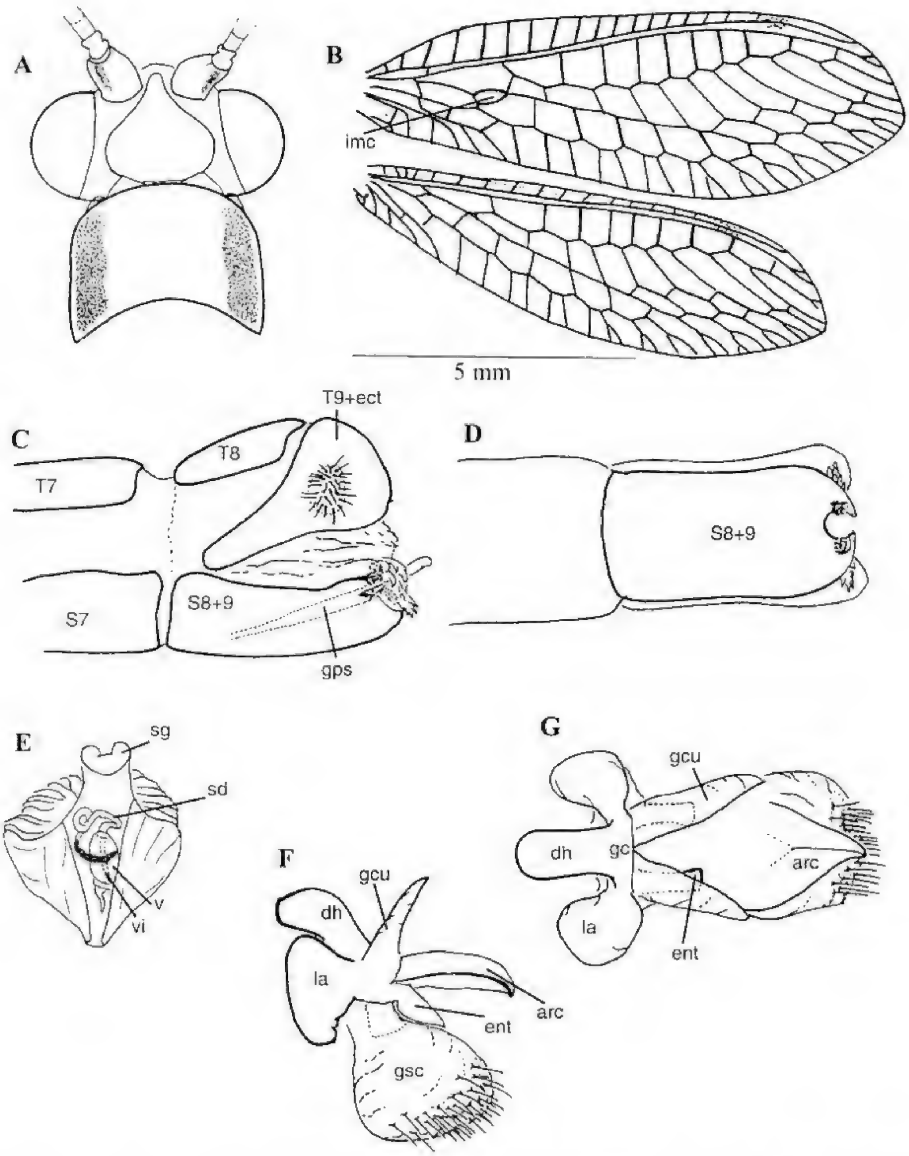


FIGURE 17. *Ceraeochrysa cubana* (Hagen, 1861). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Male abdomen apex, ventral view; E. Female genitalia; F. Male genitalia, lateral view; G. Male genitalia, dorsal view.

Pinellas Co., Indian Rocks Beach, 9 Sept. 1957, E.G. MacLeod (2♀♀ – TAMU); 10 Sept. 1957, E.G. MacLeod (2♀♀ – TAMU); Palm Harbor, 12 Feb. 1959, M. Muma (1♀ – TAMU); 11 June 1959, M. Muma (1♂, 5♀♀ – TAMU); Putnam Co., Red Water Lake, 27–28 May 1967, H.V. Weems (1♂ – TAMU); Sarasota Co., Sarasota, 6 Sept. 1958, E.G. MacLeod (1♂ – TAMU); Volusia Co., New Smyrna Beach, 10–28 June 1943, M. Wright (1?-MCZ); 1–22 July 1943, M. Wright (1?-MCZ); **MEXICO: Chiapas**, Vergel, 26 May 1935, Dampf (1?-MCZ); **Colima,** Centinela, 28 January 1930, Dampf (1?-MCZ); **Oaxaca**, Tomellin, June (♀-type of *C. tolteca*)(MCZ); **Sonora**, Navojoa, 24 March 1927, Dampf (1?-MCZ); **Tamanlipas**, El Mante, 2 August 1930, Dampf (1♂-MCZ); **Tobasco**, Villahermosa, 14 June 1928, Dampf (1?-MCZ); Frontera, 13 August 1937, Dampf (1?-MCZ); 7 June 1928 (1?-MCZ);**Veracruz**, Chavarillo, April 1899, O.W. Barrett (1?-MCZ); El Pal-

mar, 16 km W of Tetzonapa, 600 ft. [183 m], 9–15 June 1946 (1?-MCZ); **CUBA: Cienfuegos,** Soledad, 6–20 August, N. Banks (1♂ – neotype)(MCZ); P.J. Darlington 1?-MCZ); Mina Carlota, Trinidad Mtns., 22 March 1925 (1?-MCZ); **Havana**, Havana (1?-MCZ); Rio Almendares, 28 July 1923, F.Z. Cervera (1?-MCZ); 13 August 1922, F.Z. Cervera (1?-MCZ); 27 November 1923, F.Z. Cervera (1?-MCZ); San Benedito Camaguey, 11 April 1927, Cervera (1♂-MCZ); south side Pico Turquino, 3000–5000 ft. [914–1524 m], 11 June 1936, P.J. Darlington (1♂ – MCZ); P. Chivo, 18 December 1923, F.Z. Cervera (1?-MCZ); **Oriente**, Santiago, Mar Verde, June 1964, P. Alayo (2♀♀ – TAMU); **PUERTO RICO:** Rio Piedras, December 1930, (1?-MCZ); **JAMAICA**: Kingston, 27–29 August 1934, P.J. Darlington (1♀ -MCZ); Monymusk Estate, June 1959, F.D. Bennett (1♀ – TAMU); Ocho Rios, 20–24 August 1934, P.J. Darlington (1?-MCZ); Baron Hill, Trelawney, Ms. Perkins (1?-MCZ); Balaclava, 20 April, Wight (1?-MCZ); Saint Andrew, Constant Spring, 4–24 January 1920 (1?-MCZ); **CAYMAN ISLANDS:** Grand Cayman, 28 July 1980, M.E.C. Giglioli (1♂ – TAMU); west end of Georgetown, 30 April 1938, C.B. Lewis and G. H. Thompson (1?-MCZ); **DOMINICAN REPUBLIC**: San Jose de las Matas, 1000–2000 ft. [305–610 m], June 1938, P.J. Darlington (2♂♂4♀♀-MCZ). Baharona, September 1938, P.J. Darlington (1?-MCZ); **Haiti:** Hatte Lathan, 18 January, R.C. Smith (1♀- holotype of *C. damiensis* var. *jamaicensis*)(MCZ); Port-au-Prince, Schlisler's orange grove, 500 ft. [152 m], 16 November 1929 (1♂-holotype of *C. freemani*)(MCZ); **DOMINICA:** Mero, 24 July 1963, O.S. Flint, Jr. (2♂♂, 2♀♀ – TAMU); Rouseau, 22 June, C. Rous (1?-MCZ); **BARBADOS**: 92–205 (1♂- holotype of *C. imbecilla*)(BMNH); **GUATEMALA:** Cayuga, May 1915, William Schaus (1?-MCZ); **NICARAGUA**, Chinandega, Baker (1?-MCZ); **PANAMA**: Canal Zone, Barro Colorado Island, 1924. N. Banks (1?-MCZ); Juan Mina, Rio Chagres, April (1♂-MCZ); Tabernilla, 17 May 1907, A. Busck (1?-USNM); **GUYANA**:Bartica, December, Parish (1 abdomen missing – type of *C. albatala*)(MCZ); **BRAZIL:** central Brazil, Mang., 13 October 1913, R. Fischer (♀-type of *C. fischerina*)(ZMHB); **BOLIVIA: El Beni,** Riberalta, January 1922, W.M. Mann (1♂-USNM).

GEOGRAPHICAL DISTRIBUTION.— Originally described from Cuba. Otherwise known from Brazil, Jamaica, Haiti, USA, Surinam, Mexico, Dominican Republic, Barbados, Puerto Rico, Cayman Islands, Dominica, Guatemala, Nicaragua, Panama, Guyana, and Bolivia.

SPECIES RELATIONSHIPS.— This distinctive species has several unique characteristics that place it in a rather isolated phylogenetic position. The enlarged male spiracles on the abdomen are unique. The spinous projections at the apex of the male sternite VIII + IX are much more elaborate in *C. cubana* than any other known species. Males also have a rugose vertex which is otherwise only found in *C. paraguaria*, *C. scapularis,* and *C. valida.* Five species have a dorsal lobe to the male gonarcus, but it is much narrower in *C. cubana* than the other four species (*C. dislepis*, *C. everes*, *C. squalidens*, and *C. squamma*). Probably the best solution to this phylogenetic dilemma would be a DNA analysis.

REMARKS.— The original type of H.A. Hagen could not be located in USNM, and a neotype was designated by Adams and Penny (1987).

There is a specimen in the MCZ that is marked as type (no. 15739) of *Chrysopa imbecilla.* This specimen cannot be the type because it is from Cuba, not Barbados, and the authentic type (no. 92-205) is in the BMNH.

Ceraeochrysa defreitasi Penny, 2002

DIAGNOSIS.— This is one species of *Ceraeochrysa* with four dark spots on the pronotum, but no dark marks on meso- and metanota. The gonapsis with a single asymmetrical lateral arm and the median plate of arcessus with two horns are distinctive.

HEAD.— Vertex, frons, clypeus and gena yellow, unmarked. Antennal scape and pedicel pale, unmarked; flagellum pale.

THORAX.— Pronotum yellow with pair of lateral, dark reddish brown spots (Fig. 18A). Meso- and metanota yellow without markings. **Wings**: Fore wing length 14 mm. longitudinal veins pale

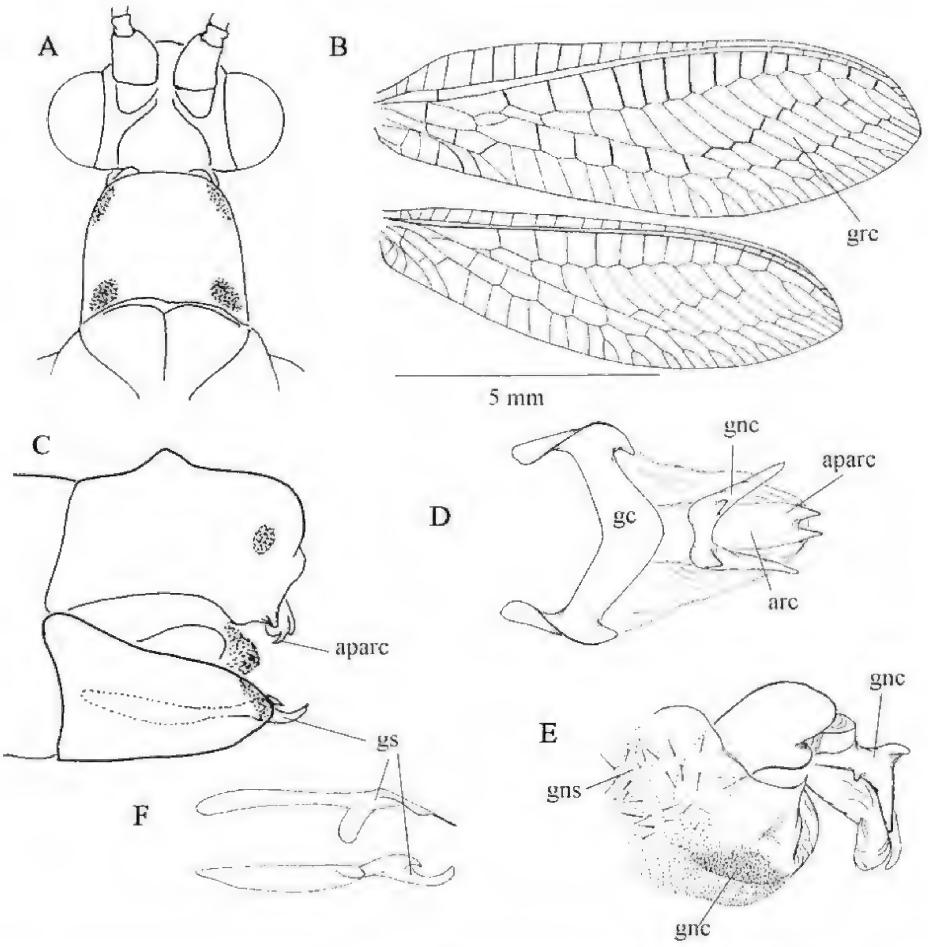


FIGURE 18. *Ceraeochrysa defreitasi* Penny, 2002. A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Gonapsis.

green. Costal and radial crossveins dark; inner and outer gradates dark, not parallel (Fig. 18B). Hindwing venation pale.

ABDOMEN.— Pale yellow with pair of small reddish spots dorsolaterally on tergites III-VI. **Male**: Tergite IX with a small pointed dorsal lobe; dorsal apodeme of ectoproct thick, with elongate ventral projection with acute apical point below ventral margin of ectoproct (Fig. 18C). Gonapsis elongate with subapical lateral lobe on left side and apical small dorsal point and more elongate ventral point (Fig. 18F). Gonarcus with ovate lateral arms and no medial points or dorsal plate (Fig. 18D, E). Arcessus with pair of lateral acute points and decurved terminal ventromedial point. Gonosaccus with extensive field of small gonocristae in aligned rows and scattered lateral gonosetae.

HOLOTYPE ♂.— **COSTA RICA: Puntarenas,** Finca Las Cruces, 8°47′28″N, 82°57′19″W, 1600 m, 14 March 1969. Joe Sheldon (INBIO).

MATERIAL EXAMINED.— see type

GEOGRAPHICAL DISTRIBUTION.— Costa Rica.

SPECIES RELATIONSHIPS.— *C. defreitasi* and *C. angulata* share a suite of characters that

separate them from all other species: the two pair of dark red spots on the pronotum; the lack of dark markings on the meso- and metanota; the male gonapsis with a small lateral lobe and tapered, thin apex. The obvious difference between the two species is the lack of dark infuscation and oftentimes small crossvein at the apical fork of CuP in *C. defreitasi*. This species also has a slightly greater number of fore wing inner gradate veins.

***Ceraeochrysa discolor* (Navás, 1914a)**

DIAGNOSIS.— This species is very near to *C. cincta*; that is, it has pale gena, palpi, antennal flagellum, and dark dorsal stripe on scape, as well as similar male genitalia, but it can be differentiated by the two spots on the pronotum rather than two stripes in *C. cincta* and the dark marks on the mesonotum.

HEAD.— Vertex, frons, clypeus and gena pale, unmarked. Antennal scape with a dorsal black stripe that does not reach fossa (Fig. 19A); pedicel and flagellum pale.

THORAX.— Pronotum with posterior pair of black circular spots (Fig. 19A); mesonotum with pair of black spots. **Wings**: Fore wing length 13. mm, width 5 mm; fairly dark; inner/outer gradates dark; costal cross veins anteriorly dark (1–7); origin of Rs, medial loop anal, cubital branches, dark (Fig. 19B). Hindwing venation pale.

ABDOMEN.— **Male**: Dorsal apodeme of ectoproct pointed (Fig. 19C). Male genitalia: gonarcus arch wide, slightly curved; gonocornua short and pointed (Fig. 19D); median plate with dorsal process; arcessus broad with lateral pointed process; apical plate not lobed.

HOLOTYPE ♂.— **PANAMA: Chiriqui,** V. de Chiriqui [Volcán Baru], 8°48′00″N, 82°31′58″W, 762–1219 m [2500–4000 ft], Champion, (BMNH).

MATERIAL EXAMINED.— **GUATEMALA:** Tres Aguas, Alta V. Paz, Barber & Schwarz (1♀-USNM); **PANAMA: Chiriqui,** V. de Chiriqui, 25–4000 ft. Champion. (1♂-holotype)(BMNH).

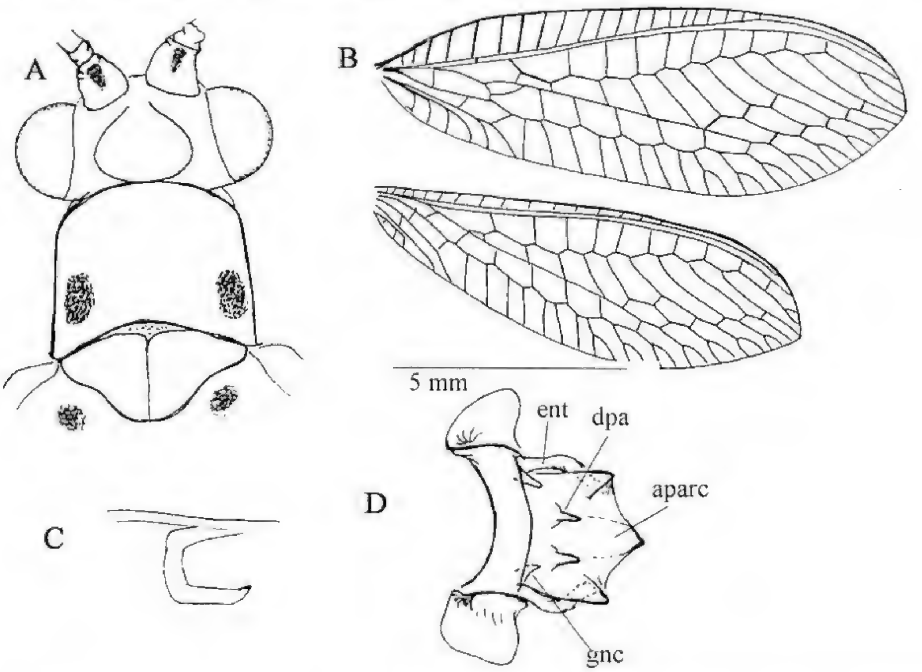


FIGURE 19. *Ceraeochrysa discolor* (Navás, 1914a). A. Head and prothorax, dorsal view; B. Wings; C. Dorsal apodeme of 9th tergite + ectoproct; D. Male genitalia, dorsal view.

GEOGRAPHICAL DISTRIBUTION.— Panama, Guatemala.

SPECIES RELATIONSHIPS.— This is one of six species that form the *cincta* group. Males of this group have a short, broad mediuncus with tripartite arcessus and two acutely pointed gonocornua widely separated on the gonarcus. The most distinctive feature of this group is the dorsal apodeme of tergite IX + ectoproct. In addition to the usual ventral branch that bifurcates near the callus cerci there is an additional decurved branch near the base. This species and *C. inbio* are the only two species of the group with reddish spots on both pronotum and mesonotum. These two species can be separated by the presence of only a single pair of dark pronotal spots in *C. discolor*, and very short gonocornua on the male gonarcus.

***Ceraeochrysa dislepis* Freitas & Penny, 2001**

DIAGNOSIS.— Males have thick-based setae at the apex of sternite VIII + IX; a thick medial field of small gonosetae on the gonosaccus; a broad dorsal hood on the gonarcus; elongate, vertically-tapered lateral arms to the gonarcus; and a pair of distinctive dorsal projections just posterior to the gonarcus that appears to be gonocornua separated from the gonarcus by a thin strip of membrane. Males of this species have no ventral projection from the ectoproct and a gonapsis that terminates in a vertical plate with a tooth. It has a central indentation of the medial plate of gonarcus and the lack of a field of tiny gonocristae laterally on the membrane below the ectoproct.

HEAD.— Yellowish green. Vertex, frons and gena pale, unmarked. Maxillary and labial palpi pale yellow unmarked. Scape yellow with lateral brown stripe widening apically (Fig. 20A); pedicel as scape; flagellum black.

THORAX.— Green. Pronotum green with a dark red lateral stripe (Fig.20A). Meso- and metanotum unmarked. **Wings**: Fore wing longitudinal veins green; costal crossveins, R-Rs crossveins, inner and outer gradates, anterior intersection of Psm-Psc crossveins, forked and unforked marginal veins, and margins near forks darkened (Fig. 20B). Length 13 mm, width 4 mm. Hindwings apically acutely pointed, green except costal crossveins; R-Rs crossveins, apex of Rs, and outer gradates dark. Length 11 mm, width 4 mm.

ABDOMEN.— Green, unmarked. **Male**: Dorsal apodeme of tergite IX + ectoproct without ventral projection (Fig. 20F). Gonapsis flattened, anterior apex a vertical plate bearing two rows of teeth (Fig. 20E). Gonarcus slightly curved with dorsomedial hood with medial indentation (Fig. 20C). Arcessus with anterior, dorso-laterally inflated lobes, a pair of small dorsal acute lobes, and decurved apical median hook with lateral lobes. Gonosaccus with lateral field of long setae and ventral fields of tiny gonocristae below setal fields (Fig. 20D). Apex of sternite VIII + IX bearing setae with thick bases arranged on small lateral lobes (Fig. 20F). **Female**: Spermatheca twisted, but not coiled (Fig. 20 G), apex with lateral alate projection. Bursa a large, transversely wrinkled sac with a pair of large accessory glands.

HOLOTYPE ♂.— **Brazil: Mato Grosso**, Itiquira, Fazenda P.E. Michelin, 17°05′00″S, 54°56′00″W, 20 January1997, S. Freitas (MZUSP).

MATERIAL EXAMINED.— **Brazil: Mato Grosso**: Itiquira, 11 January 1997, S. Freitas, (1♀- paratype)(SFC); 20 January 1997, S. Freitas(1♂- paratype)(SFC); 14 September 1996, C.H.J. Scomparin (1♀- paratype)(SFC); 4 November 1996, C.H.J. Scomparin (2♀, 1♂)(SFC); **São Paulo**: Jaboticabal, 22 November 1995 S. Freitas (1♂ – paratype)(SFC); 7 July 1996, S. Freitas (1♂ – paratype)(SFC).

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— Of the five known species in the *everes* group, with a dorsal hood on the male gonarcus, two (*C. costaricensis* and *C. squamma*) have ventral projections from the ectoproct and a gonapsis with lateral arms, while two species (*C. everes* and *C. dislepis*) have no ventral projection from the ectoproct and a gonapsis that terminates in a vertical plate with a tooth.

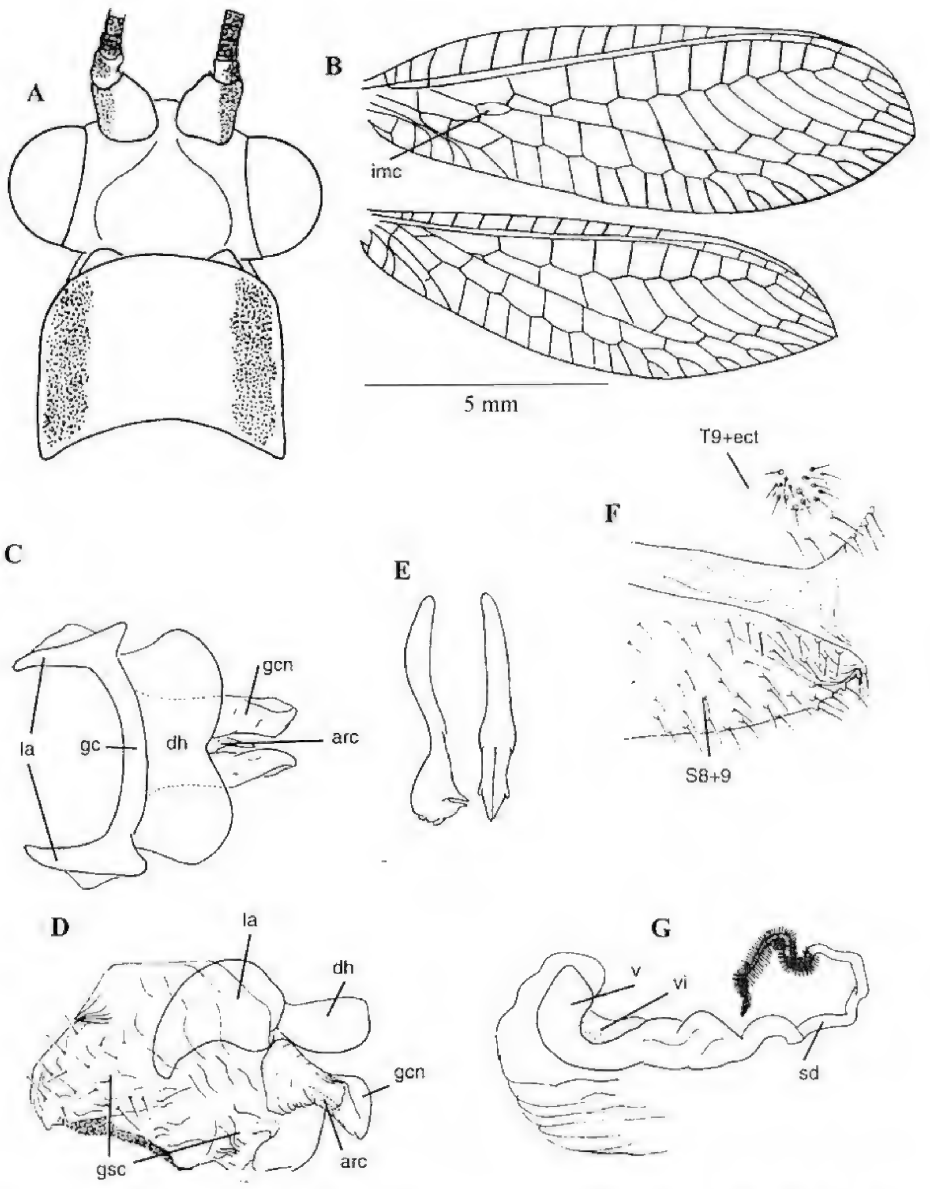


FIGURE 20. *Ceraeochrysa dislepis* Freitas and Penny, 2001. A. Head and prothorax, dorsal view; B. Wings; C. Male genitalia, dorsal view; D. Male genitalia, lateral view; E. Gonapsis; F. Male abdomen apex, detail; G. Spermatheca.

Although similar, *C. dislepis* can be separated from *C. everes* by the central indentation of the medial plate of gonarcus and the lack of a field of tiny scales laterally on the membrane below the ectoproct. *Ceraeochrysa dislepis* is most similar to *C. squalidens* in body coloration, medially indented dorsal hood of the gonarcus, and lack of lateral arms on the gonapsis. However, the gonapsis of the two species is quite different, the gonapsis of *C. squalidens* bears projections dorsally and ventrally.

***Ceraeochrysa dolichosvela* Freitas & Penny, 2001**

DIAGNOSIS.— This species has head unmarked, antennal flagellum black, scape unmarked; pronotum with red lateral stripes. The long uncoiled shape of the spermatheca is not found in any other species.

HEAD.— Vertex, frons, clypeus and gena greenish, unmarked. Antennal scape yellow-orange; pedicel black laterally; flagellum black. Maxillary and labial palpi pale.

THORAX.— Green with a pale stripe along mid-line. Pronotum green with pale brown-red lateral stripe (Fig. 21A). Meso- and metanota unmarked. **Wings**: Venation mostly green, except costal crossveins, R-Rs transverse veins and gradates black (Fig. 21B). Fore wing length 14.9 mm. hindwing venation mostly green, except R-Rs transverse veins and outer gradate series black.

ABDOMEN.— Green, unmarked. **Female**: Spermatheca extremely long, slender, uncoiled (Fig. 21C); with long spermathecal duct. Posterior part of subgenitale bilobed, with large medial anterior projection.

HOLOTYPE ♀.— **BRAZIL: São Paulo**, Jaboticabal, Faculdade de Ciencias Agrarias e Veterinárias [university campus], 21°14′40″S, 48°17′32″W. 20 January 1998 (MZUSP).

MATERIAL EXAMINED.— **BRAZIL: São Paulo**, Jaboticabal, FCAV, 20 January 1998 (1♀ – Holotype) (MZUSP); **Mato Grosso do Sul**, Corumbá, 23 July1995, S. Freitas (1♀-SFC).

GEOGRAPHICAL DISTRIBUTION.— Brazil.

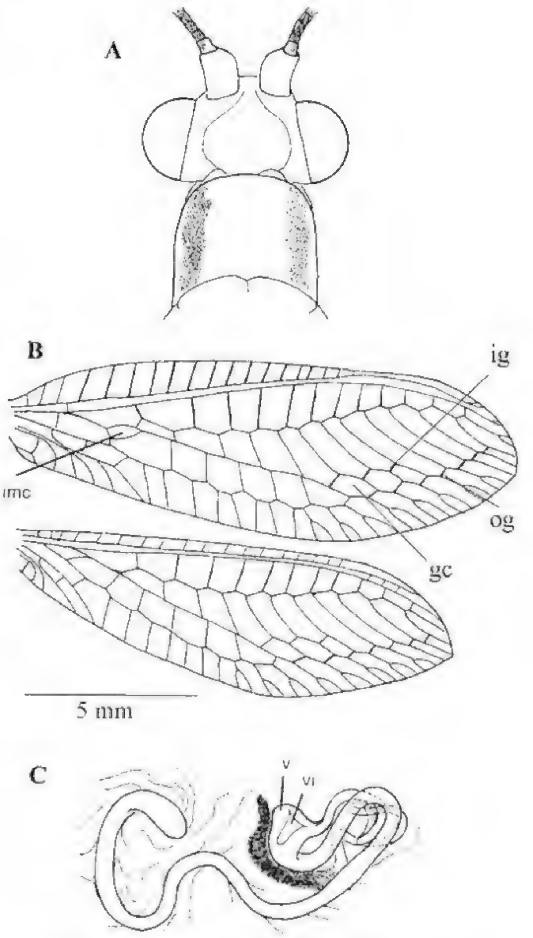


FIGURE 21. *Ceraeochrysa dolichosvela* Freitas and Penny, 2001. A. Head and prothorax, dorsal view; B. Wings; C. Spermatheca.

SPECIES RELATIONSHIPS.— The black antennae and short, parallel inner gradate series of the fore wing may align this species with *C. claveri*, but the unique long, uncoiled spermatheca of the female and lack of males makes further comparisons difficult.

***Ceraeochrysa effusa* (Navás, 1911)**

= *Chrysopa gradata* (Navás, 1913b) **New synonymy**

DIAGNOSIS.— Antennal scape with lateral dark stripe; flagellum black basally, pale apically. Pronotum with lateral red stripe. Fore wing with crossveins bordered with dark infuscation.

HEAD.— Vertex, frons, clypeus pale, unmarked. Gena dark (Figs. 22A, C, D). Antennal scape with broad black line dorso-laterally (Fig. 22A); pedicel and flagellum black basally, pale apically.

THORAX.— Pronotum short, green, with lateral dark stripe (Fig. 22A); meso- and metanota unmarked. **Wings**: Fore wing length 12 mm; longitudinal venation pale; all crossveins (transverse)

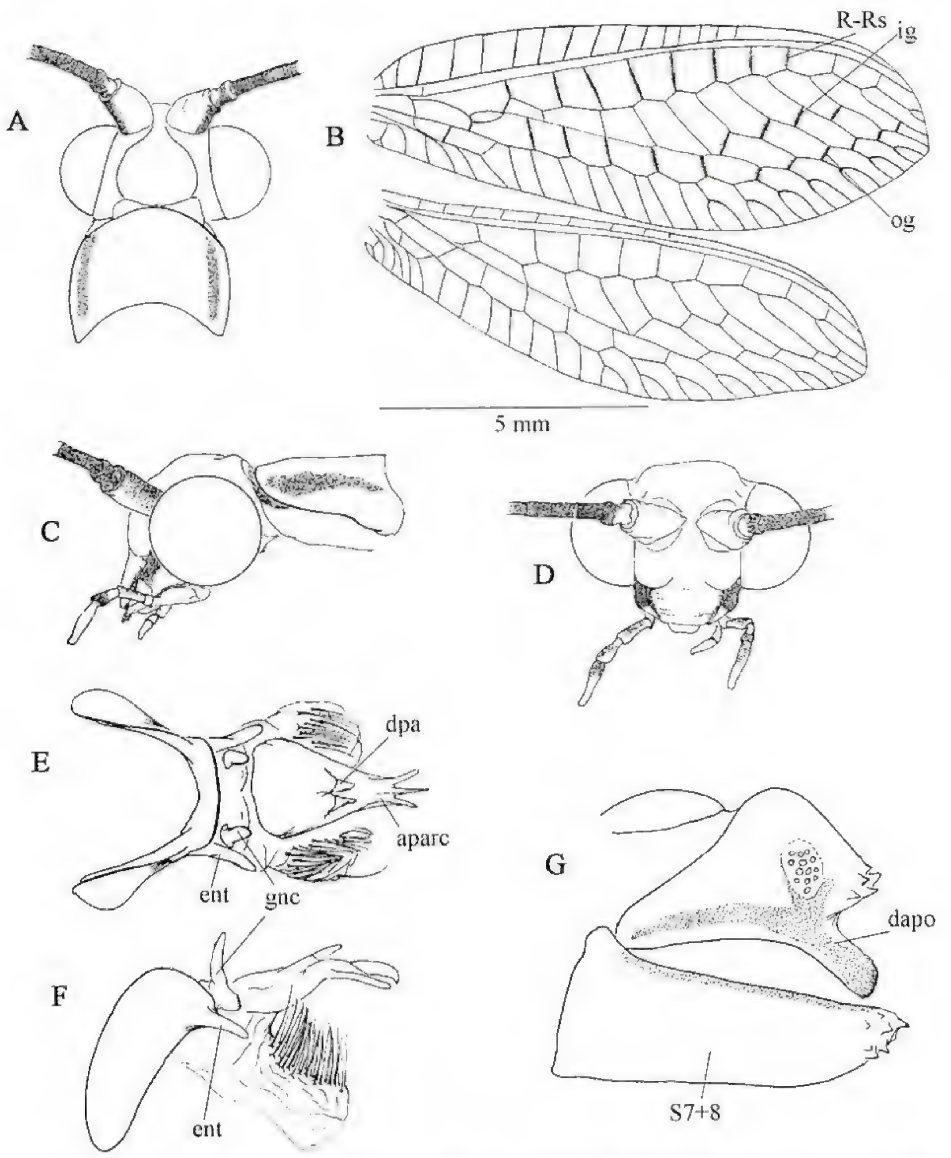


FIGURE 22. *Ceraeochrysa effusa* (Navás, 1911). A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, lateral view; D. Head, frontal view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Male abdomen, apex.

behind R_1 brown with broad clouding in membrane; gradates inner (4) outer (5) irregular in distance; dark, clouded (Fig. 22B). Hindwing length 10.8 mm; venation pale except costal crossveins and gradates dark.

ABDOMEN.— Abdomen green, without markings. **Male**: Tergite IX + ectoproct and sternite VIII + IX both with apical chalazate setae. Dorsal apodeme with dorsal branch that encircles callus cerci, and broad, thick, apically blunt, posterioventally-directed ventral branch. Gonarcus strongly arched, with elongate lateral arms and small, thin posterior branch. Gonocornua small, digitiform, widely spaced. Mediuncus and arcessus tapered posteriorly with pair of small teeth at mid-length and three apical prongs. Gonosaccus with two lateral patches of long gonosetae.

HOLOTYPE ♀.— **MEXICO:** [no specific locality or date], Sallé, 56 (MNHN).

MATERIAL EXAMINED.— **MEXICO:** [no specific locality or date](1 ♂ – holotype of *C. gradata*)(ZSM); [no specific locality or date], Sallé, 56 (1♀ – holotype of *C. effusa*)(MNHN); **HONDURAS: Olancha**, La Murralla, 24 May 1996, F.C. Andrews & A.J. Gilbert (1♂ – CAS); **Cortes**, Peña Blanca, 1–17 July 1980, P.A. Adams, 1 ? – CAS); **EL SALVADOR:** Mt. San Salvador, 8 July 1963, D.Q. Cavagnaro & M.E. Irwin (1♂ – CAS); **COSTA RICA: Guanacaste**, 3 km SE Rio Naranjo, many dates, F.D. Parker (many ♂♂, ♀♀ – EMUS).

GEOGRAPHICAL DISTRIBUTION.— Mexico, Honduras, El Salvador, Costa Rica.

SPECIES RELATIONSHIPS.— This poorly known species was described by Navás from a single female from Mexico. According to Banks (1946) it may be *C. gradata* because the latter has some of the branches of the cubitus veins that Navás figured for *C. effusa*, but the intramedian cell is not dark. The right fore wing of the type of *C. effusa* is gone, but the left one has a dark intramedian cell. The species *C. gradata* has a dark gena and a dark stripe on scape and black flagellum basally. The head of the type of *C. effusa* is poorly preserved, so that we can say little about the gena coloration. The infuscation of membrane beside all transverse veins is noteworthy. We can find no characteristics by which to separate the two species, and so we herein synonymize the two.

Males of this species have genitalia of the *lineaticornis* group that taper apically and have large patches of long gonosetae. The abdominal apex has characteristic chalazate setae. The most distinctive feature of this species is the elongate, blunt-tipped ventral branch of the dorsal apodeme.

Ceraeochrysa elegans Penny, 1998

DIAGNOSIS.— This is one of the few species with colored marks on the pro- meso- and metanota and on the abdominal tergites. The apex of posterior branch of cubital vein is swollen, darkened and margined with dark on the membrane.

HEAD.— Frons, clypeus and gena pale, unmarked. Vertex with broad, pale red, transverse spot. Antennal scape broadly marked with red; pedicel pale red dorso-laterally (Fig. 23A–D); flagellum pale; 3–4 longer setae on basal flagellomeres. Maxillary and labial palpi pale.

THORAX.— Pronotum with four red spots, the two posterior spots larger (Fig.23A, B). Meso- and metanota with two red spots. **Wings**: Fore wing length 11–14 mm, width 4–5 mm; costal crossveins anteriorly black; R-Rs crossveins black; inner gradates in irregular series, black; outer gradates black; marginal forks of veins black; posterior branches of cubital veins black, swollen and darkly margined; branch of 3A swollen (Fig. 24E). Hindwing venation pale.

ABDOMEN.— Tergites with red spots at posterior margins (Fig. 23H). **Male** dorsal apodeme of tergite IX + ectoproct wide and terminates in a hook. Genitalia (Fig. 23F, G): gonarcus thin, medial arch only slightly curved; short gonocornua; very long entoprocesses; arcessus long and narrow with apical hook; gonosaccus with field of gonocristae; gonapsis short, plate like.

HOLOTYPE ♂.— **COSTA RICA: Puntarenas**, Monteverde Biological Reserve, La Casona Station, 10°18′55″N, 84°48′16″W, 1520 m, December 1990, E. Bello (INBio).

MATERIAL EXAMINED.— **MEXICO: Tamaulipas**, El Cielo Canindo, 1 October 1995, E. Chouvakhina, on lemon (1♀ – UNAM); **COSTA RICA: Puntarenas**, Monteverde Biological Reserve, La Casona Station, E. Bello (1♂- holotype)(INBio); **Cartago**, Monumento Nacional Guayabo, Area de Conservacion La Amistad, 1100 m, July 1994, G. Fonseca, (1♀ – allotype)(INBio); Finca Las Cruces, 6 km S San Vito de Java. 1280 m, 28 September – 2 October 1986, J.E. Eger (1♀-TAMU).

GEOGRAPHICAL DISTRIBUTION.— Mexico, Costa Rica.

SPECIES RELATIONSHIPS.— Rather than a pair of lateral stripes as pronotal marks this species has two pair of spots, a characteristic shared with *C. paraguaria* and *C. nigripedis*. However,

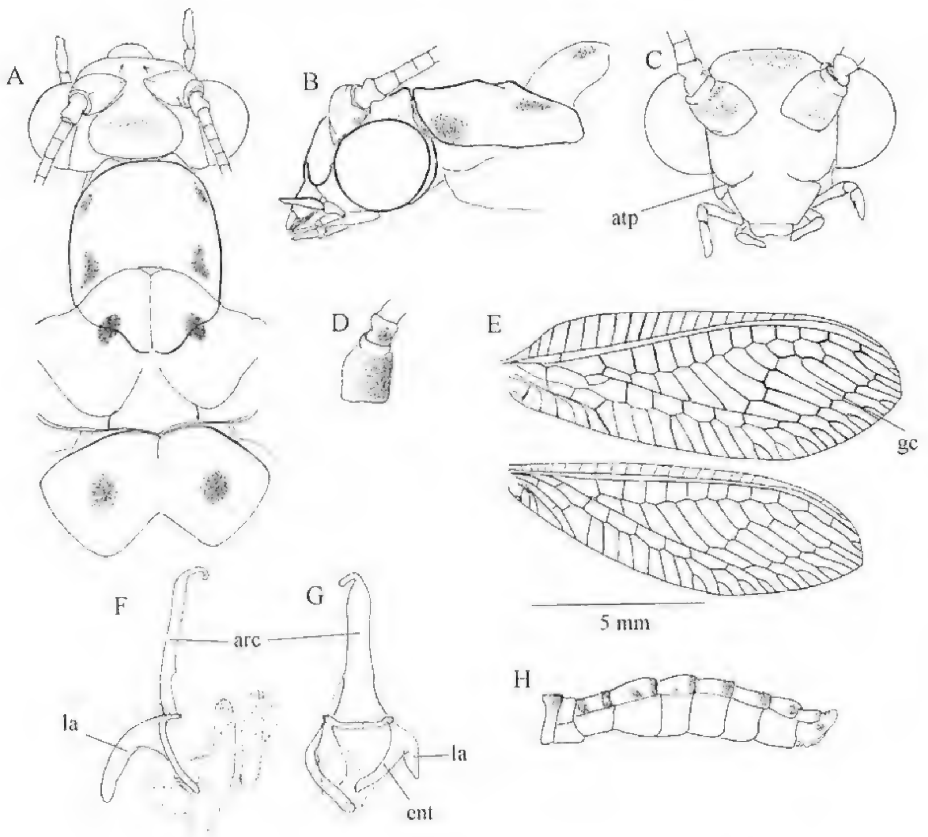


FIGURE 23: *Ceraeochrysa elegans* Penny, 1998. A. Head and prothorax, dorsal view; B. Head and prothorax, lateral view; C. Head, frontal view; D. Antennal scape and pedicel, dorsal view; E. Wings; F. Male genitalia, lateral view; G. Male genitalia, frontal view' H.Abdomen, lateral view.

C. elegans has a dark red scape stripe and spots on the abdomen. These spots take the form of red marks found along the posterior margin of each abdominal tergite.

Ceraeochrysa everes (Banks, 1920)

Chrysopa everes Banks, 1920 (French Guiana, Lectotype ♀ in MCZ)
Chrysopa furcata Navás, 1922b (Cuba, Type ♂ in MNHN)(preoccupied)
Chrysopa furculata Navás, 1923 (replacement name)
Chrysopa gundlachi Navás, 1924c (Cuba, Type ♂ in MCZ)
Chrysopa instabilis Navás, 1925a (Brazil, lectotype ♂ in MNHN)
Chrysopa jacobaea Navás, 1925b (Cuba, Type ♀ in MCZ)
Chrysopa peterseni Navás, 1929d (Colombia, Type not found)
Chrysopa petersenia Navás, 1931 (Colombia, Type not found)
Chrysopa gloriae Alayo, 1968 (Cuba, Type in IZAC, not seen)

DIAGNOSIS.— This is a species with dark antenna flagellum and narrow, red pronotal stripes. The palpi are pale and sometimes there is a dark stripe on the gena. Males have a medial hood of the gonarcus.

HEAD.— Vertex yellow to pale green, unmarked. Frons and clypeus pale yellow; gena pale yel-

low to pale brown. Maxillary and labial palpi pale. Antennal scape and pedicel diffuse pale reddish brown dorsally (Fig. 24A); flagellum black.

THORAX.— Pronotum with narrow longitudinal red stripe laterally (Fig. 24A); meso- and metanota unmarked. **Wings**: Venation green, except for some transverse veins black. Fore wing length 13 mm, width 5 mm; costal crossveins, R-Rs crossveins and gradates black (Fig. 24B); Hindwing venation black, except gradates pale.

ABDOMEN.— Green, unmarked; **Male**: Tergite IX + ectoproct without visible ventral projection of apodeme (Fig. 24I). Gonapsis flattened, apex plate-like and upturned with a row of small apical teeth and one larger dorso-apical tooth (Fig. 24H). Gonarcus strongly arched horizontally with vertically oriented, medio-dorsal hood (Fig. 24C, D); lateral arms crescent-shaped. Arcessus membranous basally with a pair of hooks and two inflated lobes; apex with a medial hook and pair of lateral, decurved and medially curved sclerotized lobes (Fig. 24E). Gonosaccus large with dense

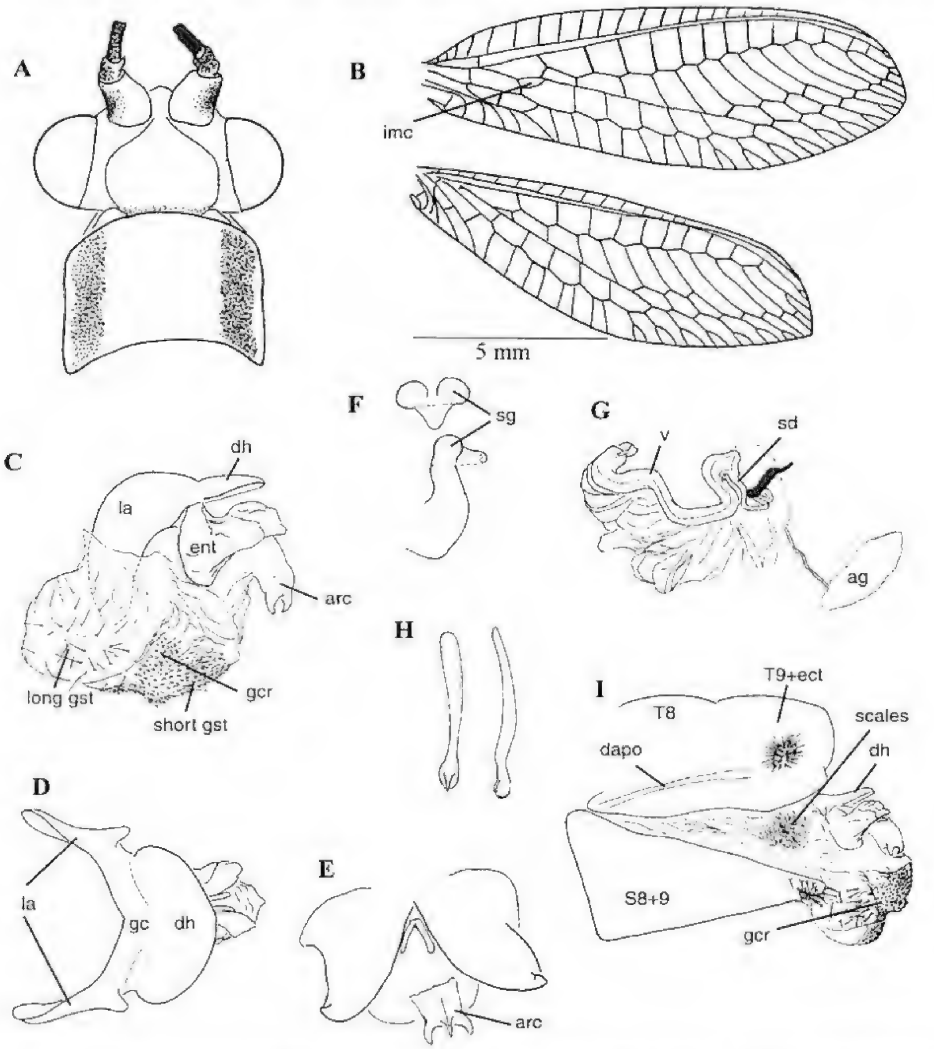


FIGURE 24. *Ceraeochrysa everes* (Banks, 1920). A. Head and prothorax, dorsal view; B. Wings; C. Male genitalia, lateral view; D. Male genitalia dorsal view; E. Male genitalia, detail, F. Subgenitale; G. Female genitalia; H. Gonapsis; I. Male abdomen apex, lateral view.

medial field of stout setae; two lateral lobes of gonosaccus with long setae, and between them a medial field of short gonosetae and a field of tiny gonocristae (Fig. 24C). Lateral to the genital atria a field of tiny scales arranged in several lines (Fig. 24I). Apex of sternite VIII + IX with large basal tubercles that bear setae arranged on two lateral lobes. **Female**: Spermatheca elongate, twisted, that opens into a transversely wrinkled bursa (Fig. 24G). Subgenitale heavily sclerotized, with a medial projection, attached to bursa by a sclerotized plate (Fig. 24F).

MATURE LARVA. – Intermandibular mark absent; epicranial mark globular, extended laterally to edge of cervical margin; lateral tubercles on abdominal segments 2–7 without marks; pronotal sclerites amber or brown; venter of head marked with brown; meso- and metanotal sclerites amber or brown (Tauber and de Leon 2001).

LECTOTYPE ♀.— **FRENCH GUIANA**: Noveau Chantier, March, M. Le Moult (MCZ).

MATERIAL EXAMINED.— **CUBA**: Santiago de las Vegas (Habana), 20 August 1924, F. Cervera (1♂-MCZ), Habana, 1925, F.E. Cervera (1♂-type of *C. furculata*)(MNHN); Santiago [de las Vegas], 18 September 1923 (1♂- type of *C. gundlachi*)(MCZ); Santiago, 6 October 1923, F.E. Cervera (1♀- type of *C. jacobaea*)(MCZ); **FRENCH GUIANA**: Noveau Chantier, March, Le Moult. (1♀-holotype of *C. everes*)(MCZ); Roches de Kourou. July, Le Moult (1♀-MCZ). **BRAZIL: Rio de Janeiro**, Nietheroy [*sic*], 12 November 1924 (1♂-holotype of *C. instabilis*)(MNHN); **São Paulo:** Jaboticabal, 20 January 1998, S. Freitas (4♂♂-SFC). **Mato Grosso:** Itiquira, 10 September 1996, C.H.J. Scomparin (2♀♀-SFC); **Amazonas:** Manaus, 6–29 November 1976, N.D. Penny (3♂♂, 5♀♀-INPA); **Rondonia:** Porto Velho, 4–5 October 1979, J.R. Arias (1♀-INPA). **Minas Gerais:** Vale do Rio Doce, 12–18 August 1978, M. Vulcano (1♂-BHMH); 15–20 October 1979 (♀-BHMH); 19–24 October 1979 (1♂-BHMH); **PARAGUAY**: Villarica, October, F. Schade (♂-MCZ).

GEOGRAPHICAL DISTRIBUTION.— Cuba, Mexico, Honduras, Colombia, Trinidad, Venezuela, Surinam, French Guiana, Brazil, Paraguay.

SPECIES RELATIONSHIPS. –The broad, medial hood of the gonarcus groups this species together with *C. dislepis*, *C. squamma*, and *C. squalidens* but can be separated from *C. dislepis* and *C. squalidens* by the presence of scales on the genital atria lateral wall and the scape has a suffused lateral spot. This species is probably most closely related to *C. squamma*, but differs by its broadly inflated gonocornua and more poorly developed scales on the membranous area below the ectoproct.

REMARKS.— No type specimen was specifically designated for *C. gloriae*, although Alayo (1968) indicated that the type was in the Instituto de Biologia (now IZAC).

In 1922b Longinos Navás described the species *Chrysopa furcata* from Havana, Cuba. This name is preoccupied by *Chrysopa furcata* Banks (1911). Navás must have realized his mistake because he subsequently (Navas 1924d, 1925c) used the name *C. furculata* from the same locality without giving any explanation as to change in names. The original description indicated that the type was in the Navás Collection (MZBS), but the type of *C. furculata* was later found in the MNHN. However, this type specimen had a collection label of 1925, three years after the original description of *C. furcata* and one year after the first use of *C. furculata*.

The type of *C. instabilis* was indicated in the original description to be in the Navás Collection (MZBS), but a member of the type series was located in the MNHN. A lectotype was desginated for this male by LeGrand et al. (2009).

Ceraeochrysa fairchildi (Banks, 1946)

DIAGNOSIS.— The head of this species has a complete absence of dark markings, although Banks (1946) mentioned "vertex each side by eye faintly suffused with rufous". The red-orange stripes laterally on the pronotum are notable. Ventral branch of dorsal apodeme attached apically

and anterioventrally oriented. The thick medial arch of the gonarcus and bulbous shape of the gonocornua are distinctive.

HEAD.— Vertex, frons, clypeus and gena, maxillary and labial palps pale; Antennae entirely pale.

THORAX.— Pronotum green with faint pale red-orange irregular lateral stripe (Fig. 25A). **Wings**: Fore wing length 12 mm, width 5 mm; costal crossveins dark except for three basal veins; R-Rs transverse veins black at base; inner gradates (3) and outer gradates (7) close together and parallel (Fig. 25B). Hindwing venation pale.

ABDOMEN.— **Male**: Tergite IX + ectoproct dorsal apodeme extends both dorsally and ventrally (Fig. 25C); apex of sternite VIII + IX with several chalazate setae (Fig. 25C). Gonarcal arch very broad; gonocornua apically expanded, dorsally flattened, with lateral down-curved point (Fig. 25E, G). Arcessus with forked dorsal process. Entire surface of gonosaccus uniformilly covered by gonocristae. Gonapsis somewhat oblique, apex forked (Fig. 25F).

HOLOTYPE ♀.— **PANAMA: Canal Zone**, Juan Mina, Rio Chagres, 11 April, G.B. Fairchild (MCZ).

MATERIAL EXAMINED.— **PANAMA: Canal Zone**, Juan Mina, Rio Chagres,11 April, G.B. Fairchild

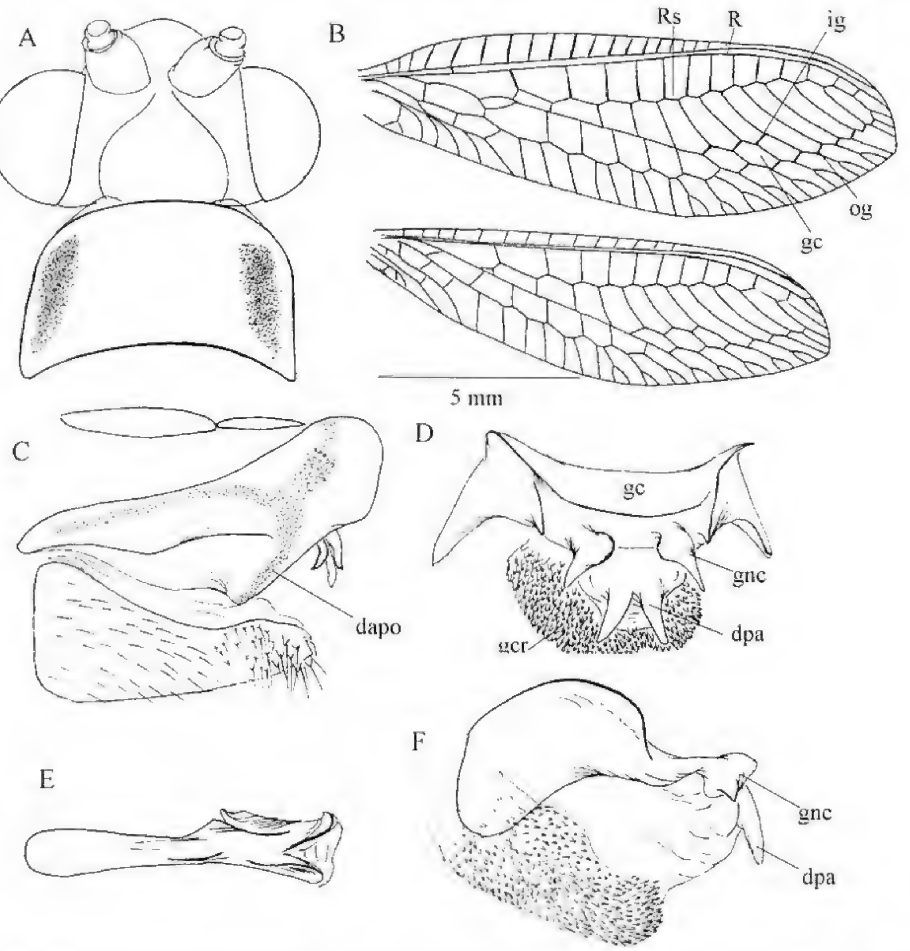


FIGURE 25. *Ceraeochrysa fairchildi* (Banks, 1946). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Male genitalia, dorsal view; E. Gonapsis; F. Male genitalia, lateral view.

(1♀-type)(MCZ); **TRINIDAD**: St. Augustine, July.1959 (1♀ – CAS); July 1959 (1♂ – CAS); Cocal, March 1959 (1♂ – ICTA). Tunapuna, 14–16 May 1959 (1♀ – CAS).

GEOGRAPHICAL DISTRIBUTION.— Panama, Trinidad

SPECIES RELATIONSHIPS.— The combination of pale antennae, pronotal stripes, and prolongation of the ventral branch of the dorsal apodeme is elsewhere found in *C. acmon*, *C. squalidens*, and *C. valida*. The gonapsis of *C. squalidens* and *C. valida* are quite different is shape from *C. fairchildi*. The ventral prolongation of the dorsal apodeme in the male genitalia portends the expanded condition found in *C. acmon*.

Ceraeochrysa falcifera Adams & Penny, 1987

DIAGNOSIS.— This species has no external remarkable features. The head and thorax have no dark markings. The unusual feature of this species is a gonapsis with curved, bristle-like process.

HEAD.— Vertex, frons, clypeus un-marked. Maxillary palpi pale, tip of apical palpimere with small black-brown mark. Antennal scape entirely pale; pedicel with brown ring; flagellum black.

THORAX.— No marks. **Wings**: Fore wing length 13 mm; pale, except in fore wing some costal veins slightly dark; radial crossveins dark in middle; inner (4) and outer (7) gradates dark (Fig. 26A).

ABDOMEN.— **Male**: No apodeme extends from tergite IX + ectoproct; a small lingulate lobe in membrane dorsally to lateral margin of ninth sternite may represent partially sclerotized apodeme (Fig. 26B). Ninth sternite deeply cleft apically, the upper corners with chalazate setae; on medial surface of corner, a lobe bears small microtrichia-like gonocristae. Gonarcus lateral arms moderately developed; arcessus broad, with apical horn flanked by lateral vertical projections; mid-dorsally on base a pair of short horns; paddle-like entoprocessus appressed to lateral surface of arcessus (Fig. 26C, D). Gonosaccus with a small dorsomedial field of short, broad gonocristae; ventrally with numerous gonosetae. Gonapsis elongate, on right side (dorsal view) with short slightly curved bristles, on left side with scythe-shaped bristle enclosed in membrane sheath (Fig. 26E, F).

TYPE ♂.— **BRAZIL: Pará**, Belém, Mocambo Forest, 14 March 1978, Malaise trap (MPEG).

MATERIAL EXAMINED.— see type.

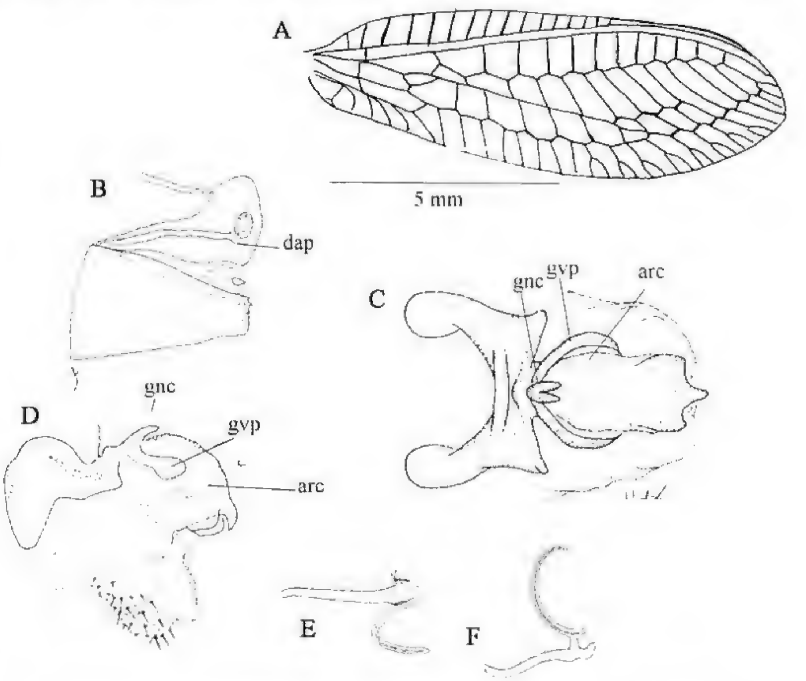


FIGURE 26. *Ceraeochrysa falcifera* Adams and Penny, 1987. A. Wings; B. Male abdomen apex, dorsal view; C. Male genitalia, dorsal view; D. Male genitalia, lateral view; E. Gonapsis, dorsal view; F. Gonapsis, lateral view. (Modified from Adams & Penny, 1987).

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— A curved, bristle-like process is also found on the gonapsis of *C. squalidens*, but in *C. falcifera*, the long process is lateral, not dorsal, and there is no bristly double crest present.

Ceraeochrysa fiebrigi (Navás, 1913a)

DIAGNOSIS.— This species has a rufous colored scape and black flagellum. The pronotum has red lateral stripe. The most distinctive character is the large bursal glands.

HEAD.— Vertex, frons, clypeus and gena olive green. Maxillary palpi rufous. Antennal scape rufous (Fig. 27A); pedicel brownish; flagellum black but gradually paler towards tip.

THORAX.— Green; pronotum transverse, two reddish brown stripes (Fig. 27A). **Wings**: Bases of wings brown. Fore wings: length 14 mm, width 4 mm; venation pale except the basal costal crossveins and all Rs sector veins which are dark; four inner gradates and seven outer gradates all pale brown, base of Rs brown; inner gradates close to outer gradates (Fig. 27B). Hindwings: venation pale.

ABDOMEN.— Rufous. **Female**: Sternite VII with sharply pointed apex. Genitalia: spermatheca "J"-shaped, dark brown, heavily sclerotized (Fig. 27D); top of the copulatory bursa deeply transversely corrugated; large rounded bursal glands; two-lobed subgenitale with large medial projection and large ventral plate (Fig. 27C).

HOLOTYPE ♀.— **PARAGUAY: Cordillera**, San Bernardino, 25°15′37″S, 57°14′35″W, [no date], Fiebrig (ZSM).

MATERIAL EXAMINED.— **PARAGUAY:** San Bernadino, Fiebrig (♀ – holotype)(ZSM); Villarica, 5 August, F. Schade (1 ? – MCZ).

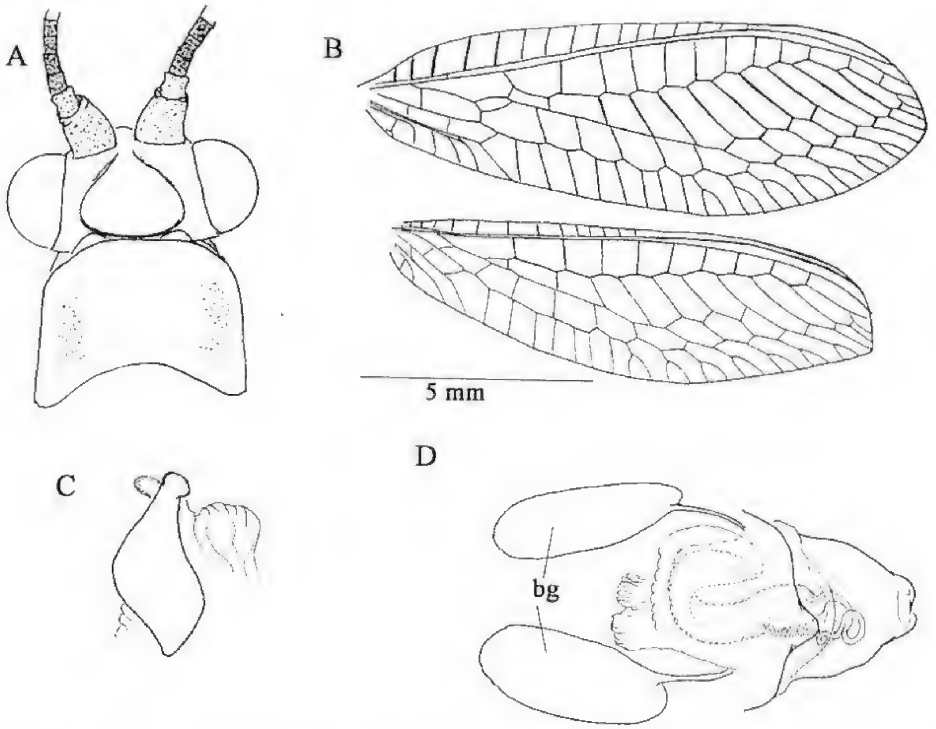


FIGURE 27. *Ceraeochrysa fiebrigi* (Navás, 1913a). A. Head and prothorax, dorsal view; B. Wings; C. Subgenitale, lateral view; D. Female genitalia.

GEOGRAPHICAL DISTRIBUTION.— Paraguay.

SPECIES RELATIONSHIPS.— This species appears to be most closely related to *C. bitacornua*. They both have dark antennae and darkened dorsal surface of the antennal scape. However, *C. fiebrigi* does not have darkly shaded fore wing gradate veins. Also, the cells between the gradate series are only about 1.5 times as long as wide, while cells of *C. bitacornua* are at least 3 times as long as wide.

Ceraeochrysa inbio Penny, 1997

DIAGNOSIS.— Antennal scape with mid-dorsal brown stripe. Pronotum with two pair of lateral brown spots; mesonotum with single pair. Male ectoprocts with recurved basal branch of dorsal apodeme. Gonocornua long, extended to base of arcessus.

HEAD.— Vertex, frons, clypeus and gena yellow, unmarked. Antennal scape and pedicel yellow, scape with longitudinal, mid-dorsal brown stripe (Fig. 28A); flagellum pale.

THORAX.— Pronotum pale green with dark brown spots in antero-lateral corners of sclerite (Fig. 28A). Meso- and metanota pale yellow with a brown stripe along suture between prescutum

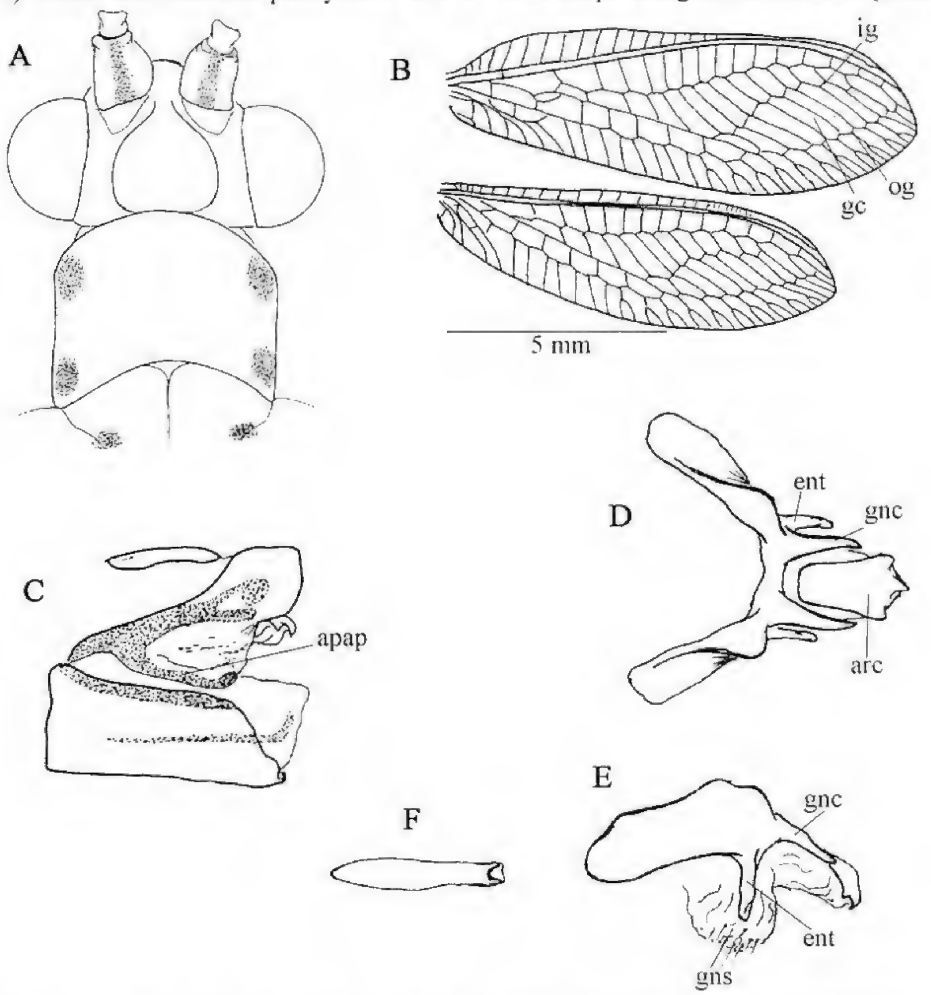


FIGURE 28. *Ceraeochrysa inbio* Penny, 1997. A. Head and prothorax, dorsal view; B. Wings. C. Male abdomen apex, lateral view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Gonapsis.

and scutum of mesonotum. **Wings**: Fore wing length 17 mm. Longitudinal veins pale green with dark crossveins except apical costal and radial crossveins pale; gradate crossveins inner (9) outer (10) dark (Fig. 28B). Hindwing length 15 mm, venation pale.

ABDOMEN.— Tergites II and III with a pair of small dark spots at posterior margin. Tergite IX + ectoproct elongate, without a ventral lobe; dorsal apodeme forked, with straight, dorsal branch apically forked around the callus cerci (Fig. 28C); ventral fork posteroventrally directed, elongate, straight, heavily-sclerotized projection that terminates in small, acute, ventral point. Sternite IX apically tapered sharply to ventral point. Gonarcus narrow medially; gonocornua tapered to relatively elongate, narrow, lateral plates (Fig. 28D). Entoprocesses elongate (Fig. 28E). Gonosaccus lacks gonocristae. Gonapsis elongate, upturned for posterior fifth, terminates in unexpanded, smoothy rounded apex (Fig. 28F).

HOLOTYPE ♂.— **COSTA RICA: Cartago**, La Amistad Biosphere Reserve, Guayabo National Monument, 1100 m, July 1994, G. Fonseca (INBio).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Costa Rica.

SPECIES RELATIONSHIPS.— Males of this species have a caudally recurved ventral fork of the dorsal apodeme and a field of gonocristae between the gonosaccus and ninth sternite, which are shared with other members of the *cincta* group. *Ceraeochrysa inbio* differs from *C. claveri* in the latter's distinctive gonapsis, which terminates in a broad, U-shaped bifurcation, and in the lack of pronounced entoprocesses. *Ceraeochrysa cincta* also has much shorter entoprocesses and a shorter, more highly curved dorsal apodeme. *Ceraeochrysa arioles* has much larger, more recurved apex of the ninth sternite. *Ceraeochrysa inbio* is very similar to *C. caligata*, except for the former's uniquely spotted pronotum and small apical point on the male ninth sternite. This is one of two species of the *cincta* group that have reddish-brown spots laterally on the pronotum. It differs from *C. discolor* in that it has two pair of pronotal spots, and the gonocornua of the male gonarcus are much longer.

Ceraeochrysa indicata (Navás, 1914a)

DIAGNOSIS.— This species has black antennal pedicel and flagellum, scape with a lateral black stripe. The fore wing has dark and bordered transverse veins. The pronotum has lateral red stripes.

HEAD.— Yellow greenish; vertex and frons pale, unmarked. Clypeus close to gena with a dark stripe. Antennal scape with black lateral stripe (Fig. 29A; pedicel black; flagellum pale.

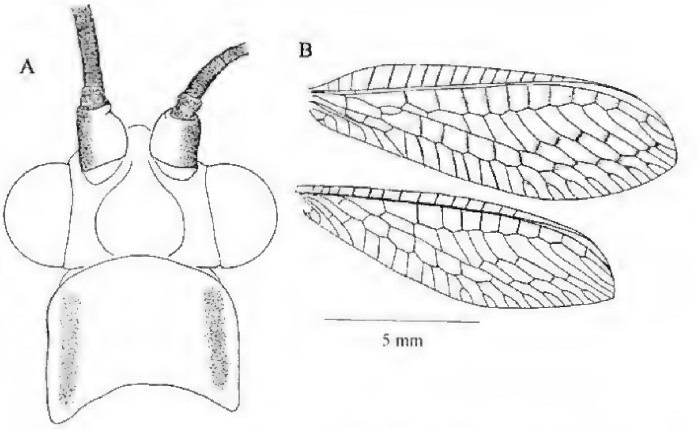


FIGURE 29. *Ceraeochrysa indicata* (Navás, 1914a). A. Head and prothorax, dorsal view; B. Wings.

THORAX.— Pronotum with dark red lateral stripes; **Wings**: Fore wing length 12 mm. Costal crossveins dark with dark margins of membrane; gradates inner (4) outer (6) and Psm-Psc crosssveins dark and darkly bordered (Fig. 29B).

ABDOMEN.— not dissected.

HOLOTYPE ♀.— **GUATEMALA: Sololá**, Zapotc, V. Atilan [Atitlán Volcano], 14°34′58″N, 91°11′09″W, 762–1066 m [2500–3500 ft.], (no date), G.C. Champion (BMNH).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Mexico, Guatemala, Costa Rica, Panama.

SPECIES RELATIONSHIPS.— This species is still poorly known and male genitalia are unknown.

Ceraeochrysa infausta (Banks, 1946)

DIAGNOSIS.— This species has black antennal pedicel and flagellum; and scape with dorso-lateral black stripe. Pronotum has lateral red stripes. Fore wing with crossveins black and bordered. The characteristic that separates it from similar species is an acute process on the prolongation of the dorsal apodeme of tergite IX + ectoproct.

HEAD.— Yellow. Vertex, frons, clypeus and gena unmarked. Maxillary palpi pale. Antennal fossa with red spot; scape with dorso-lateral black stripe (Fig. 30D); pedicel laterally black and dorsal part with black ring; first eight flagellomeres black, apical segments progressively paler.

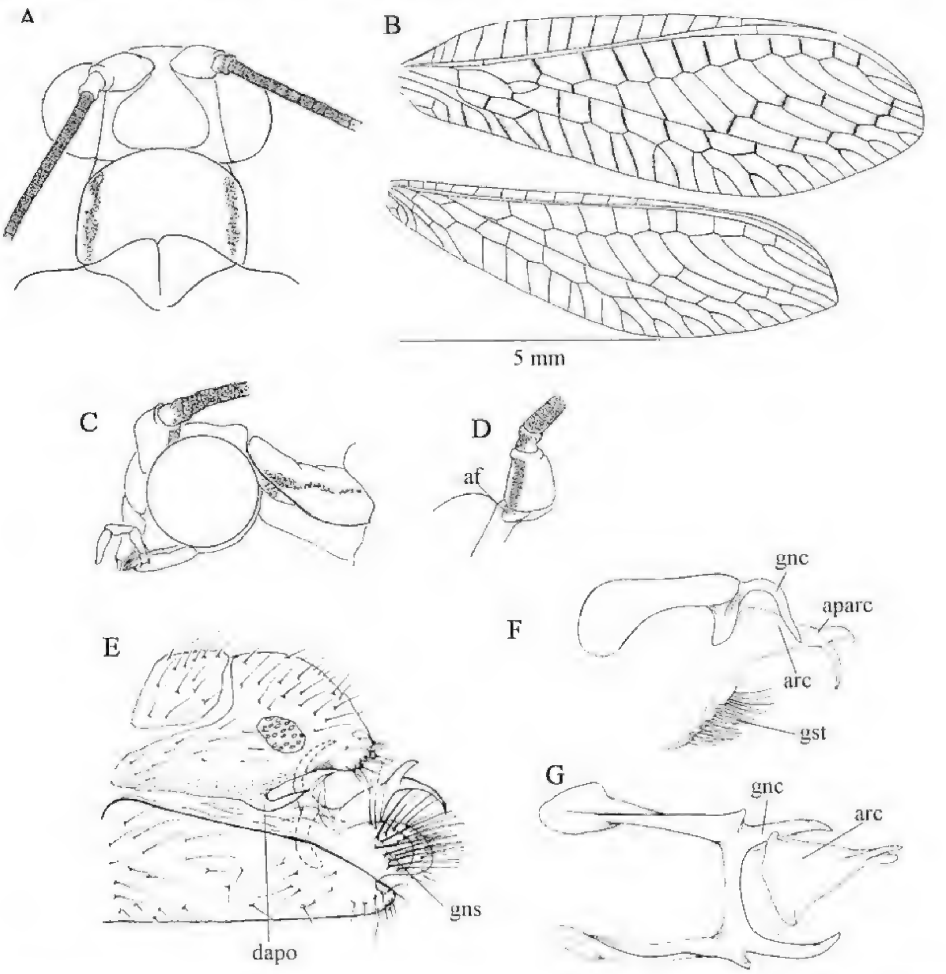


FIGURE 30. *Ceraeochrysa infausta* Banks, 1946. A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, lateral view; D. Antennal scape, dorsal view; E. Male abdomen apex, lateral view; F. Male genitalia, lateral view; G. Male genitalia, dorsal view.

THORAX.— Pronotum with irregular red stripe laterally (Fig. 30A,C). **Wings**: Fore wing length 10.5 mm; width 3.5 mm. Costal crossveins black; R-Rs crossveins, Psm-Psc crossveins, and marginal forks black and darkly bordered; inner (4) and outer (5) gradates black and darkly bordered (Fig. 30B). Hindwing venation pale.

ABDOMEN.— Pale green. **Male**: Apices of ectoproct and sternite VIII + IX with large chalazate setae. Dorsal apodeme of tergite IX + ectoproct extended ventrocaudally as a hook (Fig. 30E). Gonarcus thin. Gonocornua elongate, projected dorsally, then directed downward (Fig. 30F, G). Arcessus narrow, apically tapered to a long horn with ventral projection (Fig. 30G). Gonosaccus with two patches of long setae.

HOLOTYPE ♂.— **COSTA RICA: Limón**, Hamburg Farm, 10°07'N, 83°32'W, April, C.W. Dodge (MCZ).

MATERIAL EXAMINED.— **COSTA RICA: Limon**, Hamburg Farm, April, C.W. Dodge (1♂ – holotype)(MCZ);. **HONDURAS: Cortes**, Peña Blanca, 28 July 1976, P.A. Adams (1♂, 1? – CAS).

GEOGRAPHICAL DISTRIBUTION.— Costa Rica, Honduras.

SPECIES RELATIONSHIPS.— At first glance this species may appear to be part of the *cincta* group. However, a closer inspection will reveal that the ventral lobe of the dorsal apodeme does not originate basally, but directly below the callus cerci. The male genitalia are also not of the *cincta* type, with thin medial arch and lateral arms of the gonarcus; long, thin gonocornua; and long, prominent medial hook of the arcessus.

REMARKS.— Hamburg Farm was a site owned by the German entomologist W.H. Ferdinand Nevermann along the lower Rio Reventazon. In the early 1930's this area was lowland forest, but it is today almost entirely banana plantations.

Cereaochrysa lateralis (Guérin-Méneville, 1844)

DIAGNOSIS.— This species has a reddish dorsolateral stripe on the antennal scape, black flagellum; and pronotum with lateral red stripe.

HEAD.— Vertex, frons and gena pale, faded. Antennal scape with lateral red-brown stripe (Fig. 31A); pedicel and flagellum black.

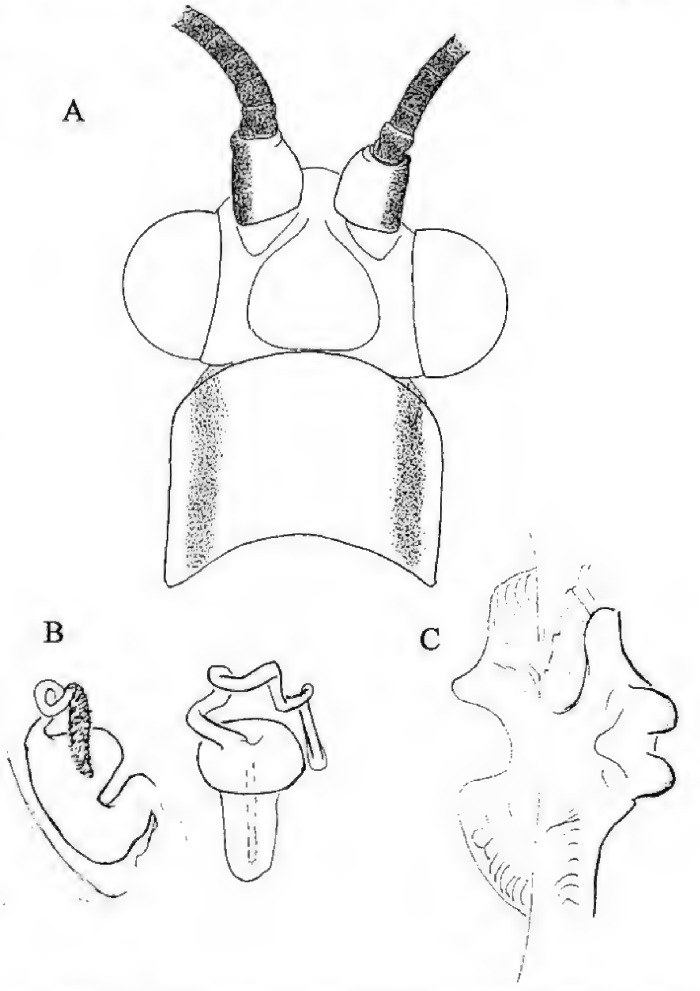


FIGURE 31. *Ceraeochrysa lateralis* (Guérin-Méneville, 1844). A. Head and prothorax, dorsal view; B. Spermatheca; C. Subgenitale.

THORAX.— Pronotum with lateral red stripes (Fig.31A); **Wings**: Fore wing length 12 mm. Costal crossveins, inner and outer gradates, Psm-Psc crossveins, and forked marginal veins dark.

ABDOMEN.— Pale green. **Female**: Abdominal tergites and sternites without apparent modifications. Spermatheca very short in relation to length of sternite VII (Fig. 31B). Subgenitale very sclerotized (Fig. 31C).

TYPE (sex unknown).— **MEXICO: Veracruz** (no specific locality, date, or collector). Presumed to be in IRSHB.

MATERIAL EXAMINED.— **COSTA RICA: San José**, San José, May – August 1910, Henry Schmidt (1♀-MZBS).

GEOGRAPHICAL DISTRIBUTION.— Costa Rica, Mexico.

SPECIES RELATIONSHIPS.— The most distinctive features of this species are the dark antennae and dark dorsolateral scape stripe, but these characteristics are shared with many other species. Nothing is known of the male genitalia at this time, so that inferences about relationships are difficult.

REMARKS.— Navás (1928) identified a series of specimens as this species in the Hamburg Museum from El Salvador, Costa Rica, and Panama that were supposedly destroyed during WWII. Surprisingly, two of them are now in the MZBS that Navás must have kept for his own collection. The ♀ is illustrated here. Additionally, Banks (1901) mentioned a specimen from Jalapa, Veracruz, Mexico, collected in August, and (Banks, 1949) specimens from Esperanza, Chiapas, Mexico 14 June; and Vergel, Chiapas, 31 May, although Banks (1946) mentions that he had not seen this species.

Ceraeochrysa laufferi (Navás, 1922a)

Chrysopa aroguesina Navás 1929a

DIAGNOSIS.— Species with pale antennae; maxillary palpi black, genae and sides of clypeus brownish black (Fig. 32A), frons with faint red spots; and vertex with some small brown marks.

HEAD.— Genae and sides of clypeus brownish black; frons with faint red spots; antennae pale; some brown spots on vertex; maxillary palpi black.

THORAX.— Pronotum with a median ivory stripe; elongate, suffused brown spots laterally; **Wings**: Fore wing length 13–15 mm; costal crossveins and R-Rs crossveins dark at the ends; gradates dark and slightly bordered; eight inner and seven outer gradates (Fig. 32B). Hindwing costal crossveins dark; R-Rs crossveins dark at the anterior ends; eight inner and seven outer gradates.

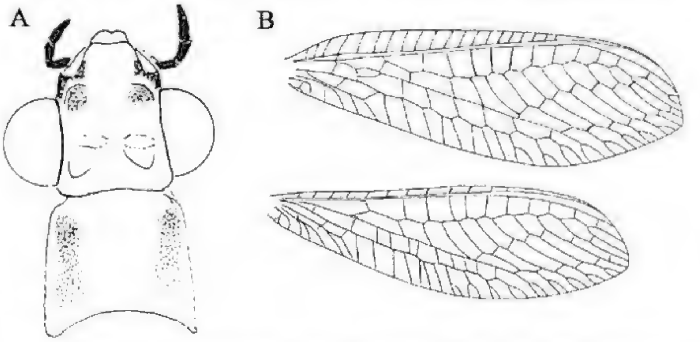


FIGURE 32. *Ceraeochrysa laufferi* (Navás, 1922a). A. Head and prothorax, dorsal view; B. Wings.

ABDOMEN.— type lacks abdomen. Type of *C. aroguesina* has short spermatheca and bilobed subgenitale.

HOLOTYPE ♂.— **COLOMBIA**: (no specific locality), 1920, Jorge Lauffer (NMHN).

MATERIAL EXAMINED.— **COLOMBIA**: 1920, Jorge Lauffer, (1♂ – holotype)(MNHN); **ECUADOR**, Azogues, D. Francisco Campos R., (1♀ – lectotype of *C. aroguesina*)(MNHN).

GEOGRAPHICAL DISTRIBUTION.— Colombia, Ecuador.

SPECIES RELATIONSHIPS.— This species has distinctive pale antennae with dark palpi and gena. The presence of so many gradate crossveins is also rather uncommon. Since the type of *C. laufferi* has lost its abdomen, no significant character states can be found to differentiate *C. laufferi* from *C. aroguesina* and so the latter name has been synonymized.

REMARKS.— The original description indicates that the type is in the Navás Collection, the remnants of which are now in the MZBS. However, the type was located in the MNHN in Paris. The measurements in the original description indicate that the type is a male (which has now lost its abdomen). A collection date of 1920 was written on the label.

The original description of *C. aroguesina* indicates that the type was from the town of Azogues, Ecuador. The name was probably meant to be "azoguesina," although this was not explicitly stated. The subsequent emendation by Brooks and Barnard (1990) was unjustified (ICZN Article 33.2.1).

LeGrand et al. (2009) transferred *C. laufferi* to *Ungla* without explanation. At this time only characters of the male genitalia can be used to separate the closely related genera *Ceraeochrysa*, *Chrysopodes* and *Ungla*. As the type specimen of *C. laufferi* is now missing its abdomen, there is no justification for removal of the species from *Ceraeochrysa* and it is herein returned to this genus.

Ceraeochrysa lineaticornis (Fitch, 1855)

Ceraeochrysa punctícornis (Fitch, 1855) (USA, Type ?, not located)
Ceraeochrysa stichoptera (Navás, 1914c)(USA, Type ? in MZBS)

DIAGNOSIS.— This species has a pale gena; black flagellar base (at least 5 flagellomeres) and scape with black lateral stripe in some specimens. Pronotum without dark lateral stripes. The fore wing transverse veins are darkly bordered.

HEAD.— Vertex, frons, clypeus and gena pale, maxillary palpi pale; antennal scape with black spot or black stripe dorsolaterally (Fig. 33A,C); pedicel dark ringed; basal part (at least 5 flagellomeres) of flagellum black, remainder gradually paler to apex.

THORAX.— Pronotum green without lateral stripes. Meso- and metanota unmarked. **Wings**: Fore wing length 14.0 mm, most transverse veins black with dark borders; longitudinal veins green (in some specimens only costal crossveins and gradates black)(Fig. 33B). Hindwing with anterior costal crossveins black. Distal part of Rs black; gradates black.

ABDOMEN.— **Male**: Dorsal apodeme with recurved dorsal branch (Fig. 33D). Gonarcal arch short, thick; lateral arms of gonarcus relatively large, hemispherical, vertically oriented. Gonocornua long, arched and acutely pointed apically with small ventral projection which may be the entoprocesses (Fig. 33E, G). Arcessus with long dorsal horns, apical plate trilobed with long acute lobes. Two lateral patches of long setae on gonosaccus (Fig. 33F). **Female**: Spermatheca short, globular, encased in quadrate apex of sternite VIII. Spermathecal duct with a double coil.

MATURE LARVA. – Intermandibular mark absent; epicranial mark globular, extended laterally to edge of cervical margin; lateral tubercles on abdominal segments 2–7 without marks; pronotal sclerites amber or brown; venter of head marked with brown; meso- and metanotal sclerites uncolored (Tauber and de Leon 2001).

HOLOTYPE ♂.— "5132" (MCZ). A series of images of the type is available on line at the MCZ website.

MATERIAL EXAMINED.— **U.S.A.: Alabama:** Mobile Co., Bellefontaine, 20 June 2004, E. Benton (1♀ – TAMU); west shore of Mobile Bay, 17–20 Aug. 1949 (1♀ – FMNH); **Arizona**: Cochise Co., Southwest Research Station, 24–27 July 1989, A.M. & N.D. Penny (5♀♀- CAS); Rucker Canyon, 4 August 1991,

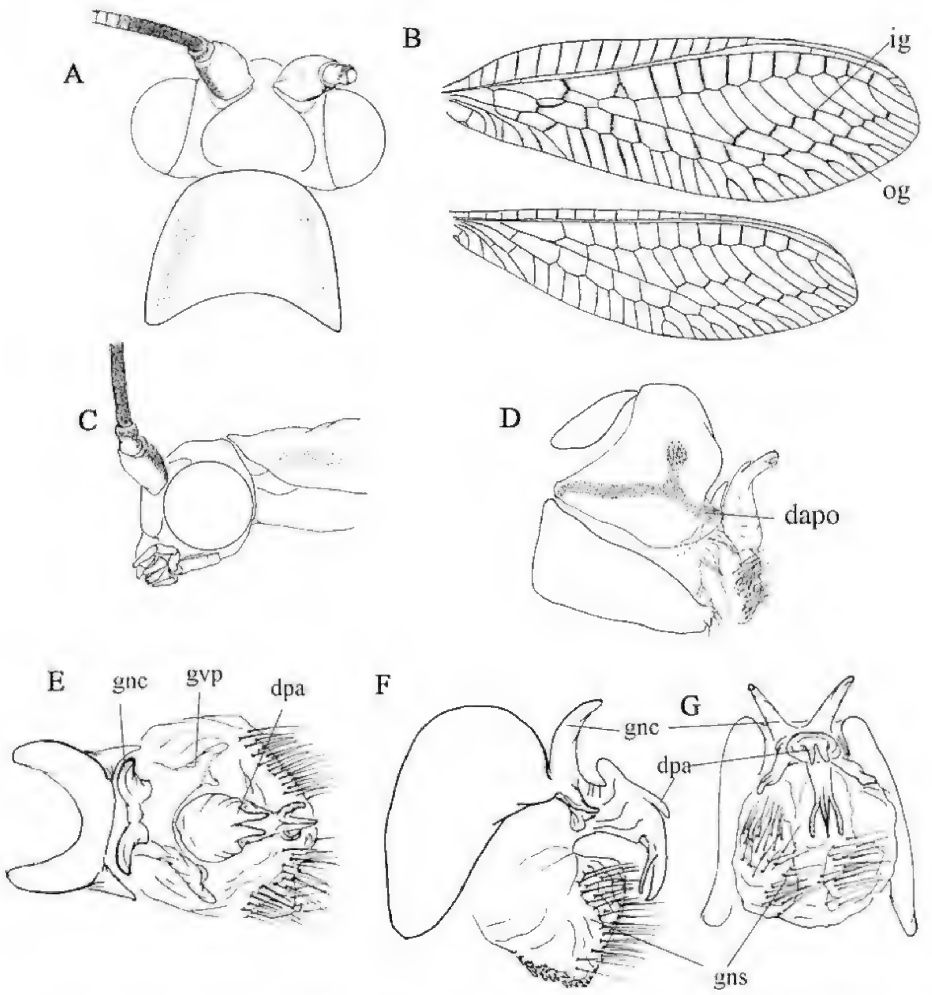


FIGURE 33. *Ceraeochrysa lineaticornis* (Fitch, 1855). A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, lateral view; D. Male abdomen, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Male genitalia, frontal view.

R. & J. Robertson (1♀ – CAS); Guadalupe Canyon, 12 July 1966, R.G. Beard (1♂ – CAS); **California:** Mendocino Co., 7.5 mi nc Covelo, 4 September 1991, J. Vindum (1♂ – CAS); **District of Columbia:** Washington, 9 Aug. 1962, B. Mather (1♂ – TAMU); Rock Creek Park, 31 May 1963, E.G. MacLeod (1? – TAMU); **Florida**: Orange Co., Wekiwa Springs State Park, burn zone, 13 April 2001, S.M. Fullerton, et al. (1♂ – CAS); 1 September 2001, S.M. Fullerton et al. (1♀- CAS); Seminole Co., Econ. Wildlife Area, scrub oak & saw palmetto, 17 September 2000, S.M. Fullerton, et al.(1♀ – CAS).); **Georgia:** Fulton Co., Atlanta, 18 Aug. 1943, H. Hoogstraal (1♀ – FMNH); **Illinois**: Champaign Co., Champaign, 19 June 1968, E.G. MacLeod (1♂ – TAMU); Mason Co., Mason State Forest, 1–2 July 1968, E.G. MacLeod & J. Sheldon (1♂ – TAMU); Union Co., Pine Hills, 25 Sept. 1965, J.C. Downey (1♂ – TAMU); **Iowa:** Crawford Co, Thul Woodland, 7 mi nw Ricketts, 3 July 2008, A.M, & N.D. Penny (1♂,1♀ – CAS); Lucas Co., Red Haw State Park, 24 August 1998. N.D. Penny (1♀ – CAS). **Kentucky**: Jefferson Co., Anchorage, 28 May 1951, B.L. Monroe (1♀ – TAMU); **Louisiana:** Grant Parish, 30 mi n Alexandria, Iatt Lake, 1–17 Sept. 1998, Brazeel & Schiff (1♀ – TAMU); Rapides Parish, Forest Hill, 4–7 Sept. 1945, R.L. Wenzel (1♀ – FMNH); 10–15 Sept. 1945, R.L. Wenzel (1♂ – FMNH); 24–29 Sept. 1945, R.L. Wenzel (1♂ – FMNH); 8–13 Oct. 1945, R.L. Wenzel (1♀ – FMNH); **Maine:** Aroostook Co., Ashland, Aug. (1♀ – MCZ); 12 Aug. (1♀ – MCZ); Ken-

nebec Co. N. Belgrade, 8 July 1991, R.E. Nelson, 1♂ – CAS); Piscataquis Co., Greenville, 2 Aug. (1♀ – MCZ); Washington Co., Kellyland, Aug. (1♂ – MCZ); **Maryland:** Baltimore Co., Catonsville, 14 July 1956, E.G. MacLeod (1♂ – TAMU); Calvert Co., Barstow, 15 July 1956, E.G. MacLeod (1♀ – TAMU); Howard Co., Dayton, 14 July 1956, E.G. MacLeod (1♀ – TAMU); Montgomery Co., Great Falls, 30 June 1956, D. Kissinger (1♂ – TAMU); Prince Georges Co., Bowie, 30 May 1954, E.G. MacLeod (1♂ – TAMU); College Park, 23 June 1956, E.G. MacLeod (3♂♂, 2♀♀, 1 ? – TAMU); 4 July 1956, I. Huber (1♀ – TAMU); 19 Sept. 1956, I. Huber (1♀ – TAMU); 25 May 1957, I. Huber (1♀ – TAMU); 30 May 1957, I. Huber (1? – TAMU); **Massachussets:** Barnstable Co., Sandwich, 19 July 1963, G.L. Bush (4♀ – TAMU); Dukes Co., West Chop, 8 August 1893 (1♀ – MCZ); Essex Co., Bradford, July 1957, N.S. Bailey (1♂, 3♀♀ – CAS); Middlesex Co., Cambridge, Sept., T. Barbour, Alteiman (3♂♂ – MCZ); Holliston, 12 June to 1 Sept., N. Banks (4♂♂, 20♀♀, 2? – MCZ); 6 August 1961, E.G. MacLeod (1♂ – TAMU); Lexington, 250 ft., 6 August 1961, E.G. MacLeod (1♂ – TAMU); 9 Sept. 1962, E.G. MacLeod (1♀ – TAMU); 11 Sept. 1962, E.G. MacLeod (1♀ – TAMU)(compared with type); 25 June 1963, E.G. MacLeod (1♀-TAMU); 7 July 1963, E.G. MacLeod (1♀ – TAMU); 18 July 1964, E.G. MacLeod (1♀ – TAMU); 21 July 1964, P.A. Adams (1♀ – TAMU); 26 August 1964 , E.G. MacLeod (1♀ – TAMU); 27 June 1965, E.G. MacLeod (1♀ – TAMU); 7 July (1♂ – MCZ); Sherborn, 7 June 1891, A.P. Morse (1♂ – MCZ); Worcester Co., Petersham, July 1941 (1♀ – MCZ); **Michigan:** Alcona Co. 5 mi N Glennie, 14 July 1996, A.M & N.D. Penny (7♂♂,1♀ – CAS); Arenac Co., 2 mi W Omer, 14 July 1996, A.M. & N.D. Penny (3♂♂,1♀ – CAS); Cheboygan Co., 12 July 1934, M.W. (1♀ – TAMU); 9 Aug. 1942, V.W. Dakin (1♀ – MCZ); Ingham Co., East Lansing, 12 July 1894 (1♀ – MCZ); Iosco Co., 2 mi n Hale, 14 July 1996, A.M. & N.D. Penny (1♂ – CAS); Kalkaska Co., 12 mi E Kalkaska, 15 July 1996, A.M. & N.D. Penny (2♂♂ – CAS); Roscommon Co., 8 July 1945, R.R. Dreisbach (1? – MCZ); **Mississippi:** Bolivar Co., 12.2 mi W Boyle, 1–15 Sept. 1998, N.M. Schiff (1♀ – TAMU); Hinds Co., Jackson, 27 June 1959, B. Mather (1♀ – TAMU); Lowndes Co., Columbus, 16 April 1964, B. Mather (1♀ – TAMU); Rankin Co., Pearl, 8 July 1962, B. Mather (1♀ – TAMU); Washington Co., Stoneville, Delta Experimental Forest, 21 June to 5 July 1998, N.M. Schiff (1♀ – TAMU); 6–21 July 1998, N.M. Schiff (1♀ – TAMU); 1–15 Sept. 1998, N.M. Schiff (2♀♀ – TAMU); 15–28 Sept. 1998, N.M. Schiff (1♀ – TAMU); 25 May to 8 June 2001, N.M. Schiff (1♀ – TAMU); **New Hampshire:** Grafton Co., Franconia (2♂♂, 1♀ – MCZ); **New York**: Albany Co., E.N. Huyck Preserve, 8 August 1961, E.G. MacLeod (1♂ – TAMU); **North Carolina**: Cumberland Co, Fort Bragg, 23–25 August 1967, J.D. Birchim (1♂ – CAS); Yancey Co., Blue Ridge Parkway, Crabtree Meadows Campground, 3300 ft., 21 June 1962, G.L. Bush (1♂ – TAMU); **North Dakota**: Pembina Co., Tetrault Woods State Forest, 19 July 1996, A.M. & N.D. Penny (1♂1♀ – CAS); **Ohio:** Summit Co., Akron, 25 September 1997, J. Schweikert (1♀ – CAS). **South Carolina:** Aiken Co., Aiken, 18 Sept. 2006, H. Cony (1♀ – FMNH); Greenville Co., Greenville, 27 Aug. 1957, E.G. MacLeod (1♂ – TAMU); **Tennessee:** Henry Co., Paris, Camp Tyson, 28 Aug. 1943, R.L. Wenzel (1? – FMNH); **Texas:** Bastrop Co., Stengl Ranch, 9.5 km n Smithville, 22 Sept. 2002 J.D. Oswald (1♂, 1♀ – TAMU); Bexar Co., Ebony Hill Research Station, R.O. Kendall, 10 July 1991 (1♀ – TAMU); 24 Sept. 1992 (1? – TAMU); 17 Aug. 1993 (1♂ – TAMU); 31 Aug. 1993 (1♂ – TAMU); 2 Sept. 1993 (1? – TAMU); 5 Sept. 1993 (1? – TAMU); 6 Sept. 1993 (1♂ – TAMU); 10 Sept. 1994 (1♂ – TAMU); 19 June 1994 (1♀ – TAMU); 20 June 1994 (1♂ – TAMU); 1 June 1995 (1? – TAMU); 6 June 1995 (1♂ – TAMU); 10 June 1995 (1♀ – TAMU); 12 June 1995 (1? – TAMU); 21 June 1995 (1♀ – TAMU); 8 June 1996 (1♂ – TAMU); 12 July 1999 (1♀ – TAMU); Kerr Co., Kerrville, 18 August 2002 (1♀ – TAMU); Leon Co., 8.8 km n Flynn, 11 Sept. 2001, J.D. Oswald (1♀ – TAMU). **Virginia:** Alexandria, 1–20 August 2007, O.S. Flint, Jr. & P.H. Arnaud, Jr. (1♀ – CAS); Augusta Co., Mt. Solon, July 1951, W.S. Murray (1♀ – TAMU); Giles Co., Mountain Lake, 12 July 1940, L. J. And M.J. Milne (1♂ – TAMU); **West Virginia**: Hardy Co., 3 mi ne Mathias, 26 June – 9 July 2001, D. Smith (1♀ – TAMU); 10–24 July 2001, D. Smith (1♀ – TAMU); **Wisconsin**: Bayfield Co., 2 mi e Iron River, 17 July 1996, A.M. & N.D. Penny (1♀ – CAS).

GEOGRAPHICAL DISTRIBUTION.— Southeastern Canada, eastern and southern USA. Infrequent in western USA.

SPECIES RELATIONSHIPS.— This is a quite variable species. Two of the most distinctive markings can be absent on some individuals: the dark brown lateral stripe on the antennal scape and the narrow brown or reddish brown lateral stripes on the pronotoum.

There are also some individuals that have a dark genal spot. Banks (1903) gave the latter form a name, *C. columbiana*, but Bram and Bickley (1963) later synonymized it. However, we have found some consistent differences in the male genitalia that warrant resurrection of Banks' species. Another complicating factor is that an aberrant specimen of the same species with a quadrate intramedian cell was described as *Allochrysa parvula*. This specimen was described in the same article as *C. columbiana*, and had earlier pagination, so that it has nomenclatural priority.

REMARKS.— Neither of the names *C. puncticornis* nor *C. stichoptera* were listed in the extensive synonymy in Adams' (1982) original description of the genus, although Bickley and MacLeod (1956) had previously synonymized *C. stichoptera* and Banks (1907) had synonymized *C. puncticornis*. We have upheld those synonymies here.

Ceraeochrysa michaelmuris Adams & Penny, 1987

DIAGNOSIS.— Head pale without marks; small size (fore wing length 9 mm); wings with few gradates; mesonotum with two dark round marks. The most distinctive characteristic is the paired spinous lobes at the end of the male ninth sternite.

HEAD.— Pale, unmarked; antennae and palpi also pale.

THORAX.— Pronotum without marks. Mesonotum with lateral dark spots. **Wings**: Fore wing length 9.0 mm, all transverse veins dark including gradates; also dark: most longitudinal veins at

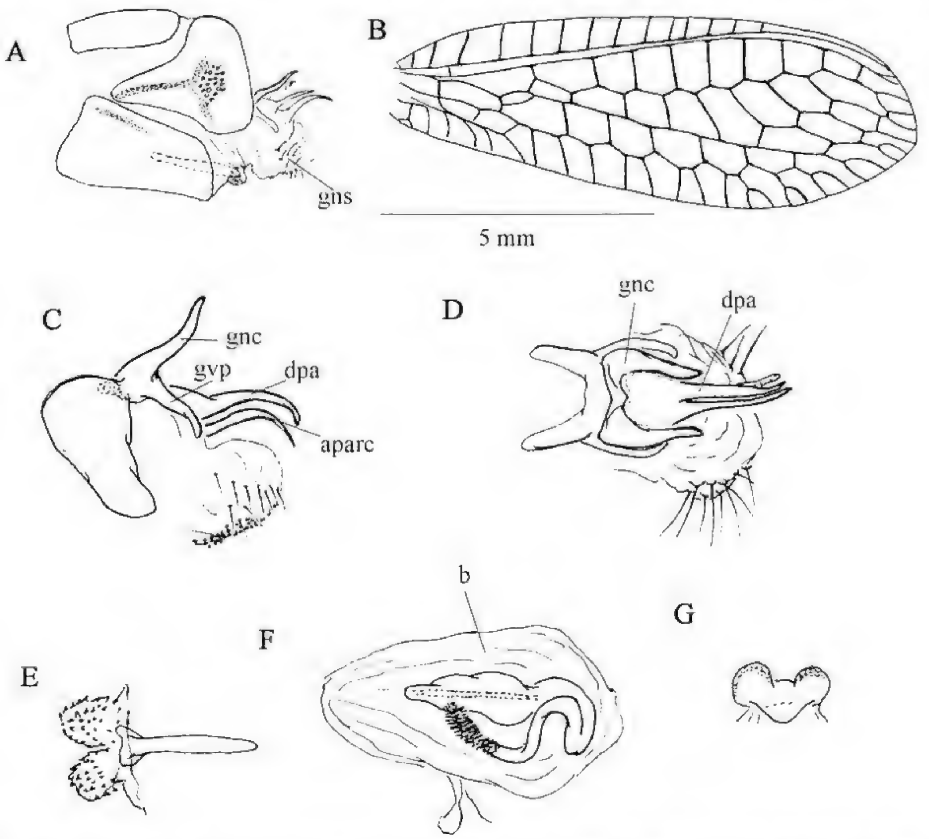


FIGURE 34. *Ceraeochrysa michaelmuris* Adams and Penny, 1987. A. Male abdomen apex, lateral view; B. Wings. C. Male genitalia, lateral view; D. Male genitalia, dorsal view; E. Gonapsis; F. Female genitalia; G. Subgenitale. (Modified from Adams and Penny, 1987).

intersection of transverse veins, base of Rs+Ma, and several branches of Rs at base (Fig. 34B). Hindwing: apex of radius and middle of Rs+Ma dark; costal, radial and gradate veins pale brown.

ABDOMEN.— **Male**: Apodeme of tergite IX + ectoproct not extended ventrally (Fig.34A). Gonarcus large; medial arch moderately wide, with long, narrow gonocornua and a ventral branch downwardly projected (Fig. 34C,D); arcessus dorsally with two long processes and at the apex an unpaired, thin process; gonosaccus with few long setae and gonocristae. Gonapsis elongate with caudal Y-shaped darkly stained arms (Fig.34E). Beyond apex of sternite IX are two oval lobes, tilted downward medially, and covered with large, short, sharp-tipped gonocristae gradually modified laterally to microtrichia with enlarged bases. **Female**: Without modification on sternite VII; subgenitale short, with round caudal lobes and short basal lobe (Fig. 34G); well set off from membranous area connected to seventh sternite. Spermatheca short, pyriform, open to bursa along straight dorsal slit (Fig. 34F).

HOLOTYPE ♂.— **BRAZIL: Amazonas**: Manaus, 3°01′52″S, 59°56′43″W, 6 January 1979, J.A. Rafael (INPA).

MATERIAL EXAMINED.— **BRAZIL: Amazonas**, Manaus, J.A. Rafael, 6 January 1979 (1♂ – holotype)(INPA); 14 October 1978 (1♀ – allotype)(INPA).

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— The bilobed apex of the male gonapsis is distinctive. This character state is also found in *C. claveri*, but in the latter species the lobes are narrow, and it has the basal ventral branch of the dorsal apodeme characteristic of the *cincta* group, a state not found in *C. michaelmuris*.

Ceraeochrysa montoyana (Navás, 1913a)

DIAGNOSIS.— Dark antennae; the scape has a double stripe; and the spermatheca is U-shaped. The two-striped scape of *C. montoyana* is the most distinctive characteristic.

HEAD.— Vertex golden yellow. Frons, clypeus, maxillary palpi, and gena pale, unmarked. Antennal flagellum black; scape yellow with two narrow stripes, one on the lateral side, and one broader stripe dorsally (Fig. 35A).

THORAX.— Narrow lateral red stripes on pronotum (Fig. 35A). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 15 mm, venation mostly green, except costal, R – Rs, Psm-Psc crossveins, apical forks and anal crossveins dark (Fig. 35B).

ABDOMEN.— Green, without dark marks. **Female**: Spermatheca U-shaped, short, with long spermathecal gland (Fig. 35C). Subgenitale with two broad lobes (Fig. 35D).

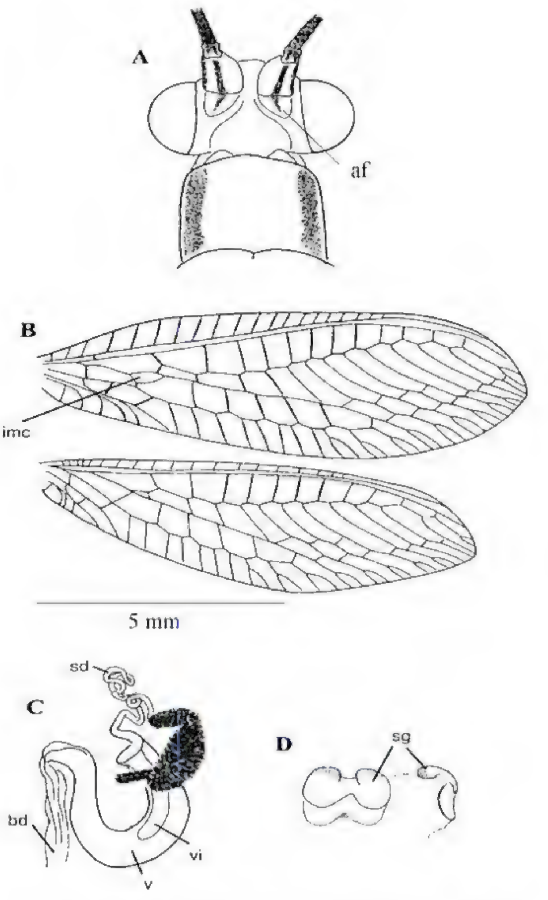


FIGURE 35. *Ceraeochrysa montoyana* (Navás, 1913a). A. Head and prothorax, dorsal view; B. Wings; C. Spermatheca; D. Subgenitale.

HOLOTYPE ♀.— **PARAGUAY: Cordillera**, San Bernardino, 25°15′27″S, 57°14′44″W, (no date)(ZSM).

MATERIAL EXAMINED.— **PARAGUAY: Cordillera**, San Bernardino, (no date), Navás, S.J. (1♀)(type); **BRAZIL: São Paulo**, Jaboticabal, 25 March 1999, S. Freitas (1♀- SFC).

GEOGRAPHICAL DISTRIBUTION.— Paraguay, Brazil.

SPECIES RELATIONSHIPS.— This species is closely related to other *cincta* group species that have dark antennae, such as *C. claveri*. In *C. claveri* the scape has a single stripe that continues onto the antennal basal membrane, and the spermatheca of *C. claveri* is not U-shaped. The distinctive double scape stripe is elsewhere found in *C. arioles* and the Florida population of *C. cincta*.

Ceraeochrysa nigripedis Penny, 1997

DIAGNOSIS.— This species has a peculiar and uncommon spotting pattern on the thorax: four small, dark spots on the pronotum; two spots on the mesonotum; and two spots on the metanotum; and darkened apical tarsal segments.

HEAD.— Vertex, frons, clypeus and gena pale without marks. Antennae pale.

THORAX.— Pronotum pale with pair of small, dark marks on anterior and pair at posterior margins (Fig. 36A). Meso- and metanota pale yellow, with a pair of round dark brown spots at suture

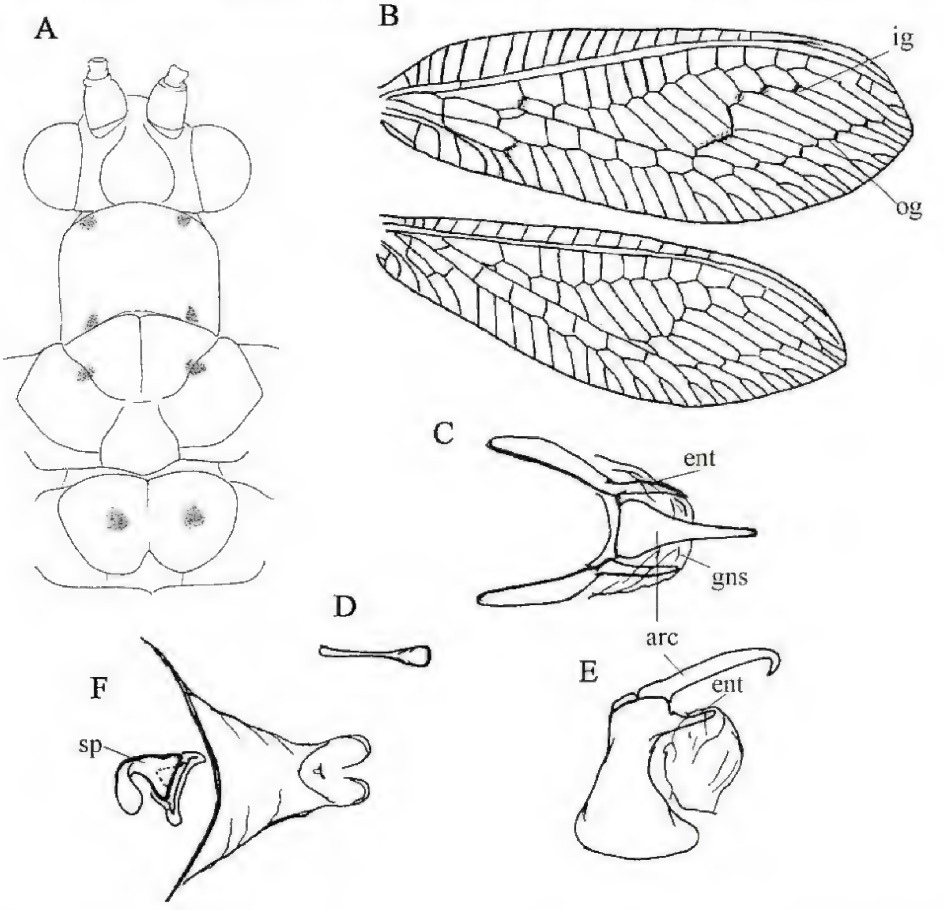


FIGURE 36. *Ceraeochrysa nigripedis* Penny, 1997. A. Head and thorax, dorsal view; B. Wings; C. Male genitalia, dorsal view; D. Gonapsis; E. Male genitalia, lateral view; F. Female genitalia.

between prescutum and scutum on mesonotum and laterally on scutum of metanotum (Fig. 36A). Each leg pale yellow except apical tarsomere contrastingly dark brown. **Wings**: Fore wing length 13 mm. Longitudinal veins pale green; crossveins and apical twigging dark brown, except for apical costal crossveins. Gradate veins black with strong infuscation on membrane along inner series. Seven inner and eight outer gradate veins (Fig. 36B). Intense dark markings at apex of 1A, posterior cubitus and Cua-Cup crossveins, to form a point of visual attraction on the wing. Hindwing venation pale, except most gradate veins dark.

ABDOMEN.— Pale yellow, unmarked. **Male**: Ectoproct + tergite IX short and broad, with scattered setae with thickened bases; dorsal apodeme simple, extends to callus cerci, without ventral lobe. Sternite VIII + IX with broad, dorsolateral, subapical projection; numerous setae with thickened bases. Gonarcus medial arch narrow, with broad lateral arms (Fig. 36C, E). Entoprocesses laterally embedded in simple, membranous gonosaccus. Arcessus very long, narrow, straight, with decurved apical point. Gonapsis elongate with slightly upturned and expanded, smoothly rounded apex (Fig. 36D). **Female**: Subgenitale broadly heart-shaped, with deep central cleft. Spermatheca strongly arched anterior to spermathecal ducts (Fig. 36F).

HOLOTYPE ♂.— **COSTA RICA: Puntarenas**, Monteverde Biological Reserve, La Casona Station, 10°18′57″N, 84°48′23″W, 1520 m, November 1991, N. Obando (INBio).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Costa Rica.

SPECIES RELATIONSHIPS.— *C. nigripedis* appears to be most closely related to *C. tauberae*, with which it shares an elongate, straight arcessus and dark area of visual attraction on 1A at the base of the fore wing.

Ceraeochrysa nigripes Adams and Penny, 1987

DIAGNOSIS.— Black tibiae and a red, medial thoracic stripe. Males also possess gonocristae over the entire gonosaccus.

HEAD.— Vertex yellowish brown with transverse red band across middle (Fig. 37A); anterior diagonal red lines parallel posterior margins of antennal fosaa. Frons and genae yellowish brown, unmarked. Maxillary palpi yellow. Antennal scape and pedicel yellow, scape with dark basal ring on dorsal surface; flagellum black for about one fourth its length.

THORAX.— Pronotum red medially, yellow laterally and pink at lateral margin. Mesoprescutum with medial red area; mesoscutellum and metanota blackish red medially and yellow laterally; some specimens with irregular black marks. **Legs**: With tibiae black for sligthy more than half, to almost entire length. Fore tibia less darkened, with a line on outer surface, or unmarked. **Wings**: Fore wing length 12 mm, venation pale with veins darkened on apical half of wing. Costals dark, inner (6) and outer (8) gradate veins dark, parallel series, marginal forks dark (Fig. 37B). Hindwing venation pale.

ABDOMEN.— Yellow to pale green laterally and red medially on tergites II to VI. **Male**: Apodeme of tergite IX + ectoproct without ventral projection; a small dentate lateral lobe on membrane below tergite and dorsal to sternite VIII + IX (Fig. 37C). Gonapsis long, slender, without apical horn or projections. Gonarcus complex with broad lateral arms, broad, strongly-arced medial arch (Fig. 37E). Gonocornua narrowly separated as two, acute, dorso-caudal projections with small rounded lateral processes (Fig. 37D); entoprocesses vertical; arcessus elongate, triangular, acute, with deflexed apex. Gonosaccus with numerous gonocristae; gonosetae sparse. **Female**: Bursa transversally wrinkled posterodorsally; bursal gland reservoirs oval, ducts joined to bursa somewhat posterolaterally (Fig. 37F). Spermatheca J-shaped, open for nearly its entire length into diag-

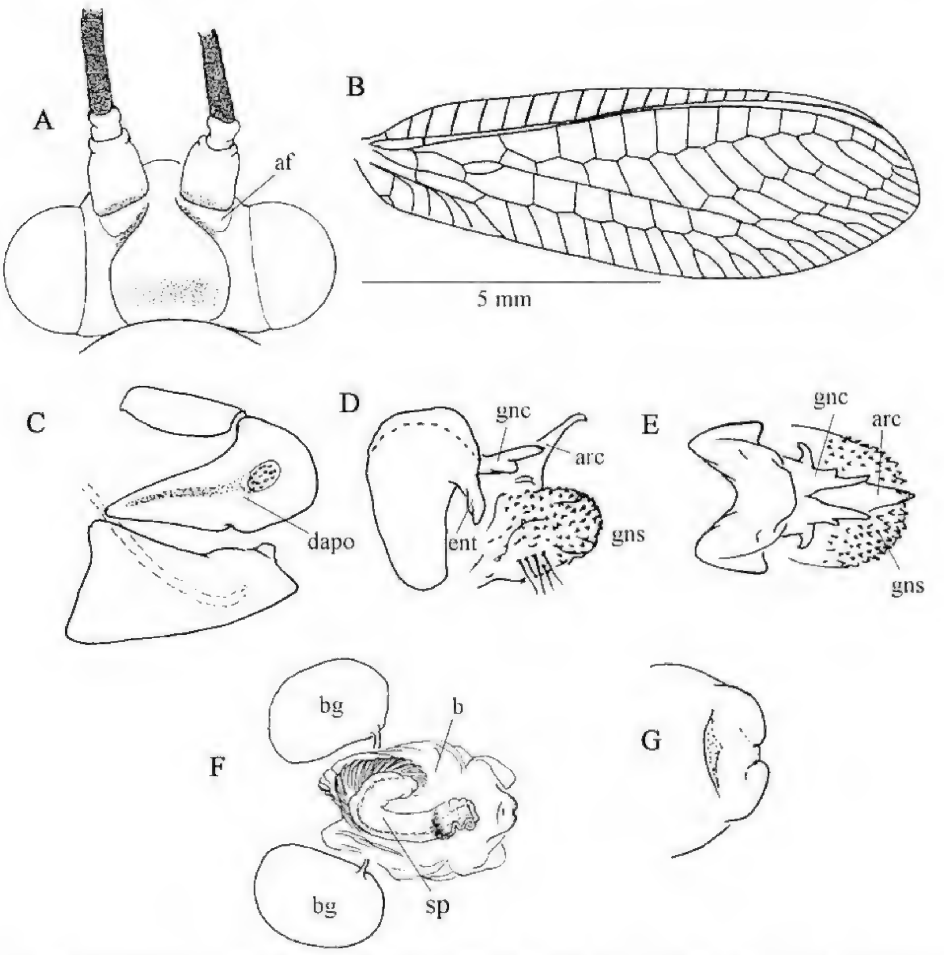


FIGURE 37. *Ceraeochrysa nigripes* Adams and Penny, 1987. A. Head, dorsal view; B. Wing; C. Male abdomen apex, lateral view; D. Male genitalia, lateral view; E. Male genitalia, dorsal view; F. Female genitalia; G. Subgenitale. (Modified from Adams and Penny, 1987).

onally pleated extension of bursa; spermathecal duct short. Subgenitale ventral lip with notch on anterodorsal surface (Fig. 37G).

HOLOTYPE ♂.— **BRAZIL: Rondonia**, Vilhena, 12°44′17″S, 60°07′04″W, 6 November 1979, N.D. Penny & J.R. Arias (INPA).

MATERIAL EXAMINED.— **BRAZIL: Rondonia**: Vilhena, 6 November.1979. N.D. Penny & J.R. Arias (1♂ – holotype)(INPA); **Amazonas:** Manaus, 1–29 August 1978 (2♂♂, 1♀- INPA); 7 February 1978, (1♀-INPA); 18 August.1978, (1♂-INPA); J.R. Arias, 12 May 1977, E. Castellon, (1♀-INPA); **Pará**: Igarape Assu, December 1911, H.L. Parish, (1♀-MCZ); **Acre**: Cruzeiro do Sul, Ilha Florianopolis, 15–16 May 1981, J. Arias (1♂-INPA).

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— This species is unique among species of *Ceraeochrysa* in that it has black tibiae and a red, medial thoracic stripe in a genus where dark pronotal markings are invariably lateral. Males are unusual in that the gonosaccus has so many gonocristae and so few gonosetae, similar to *C. fairchildi* and *C. squalidens*, but otherwise they don't appear closely related.

***Ceraeochrysa paraguaria* (Navás, 1920)**

DIAGNOSIS.— Four discrete dark spots on pronotum. Male genitalia with two elongate, spinous lobes at apex of sternite VIII + IX; gonosaccus with chalazate gonosetae.

HEAD.— Vertex, frons, clypeus and gena pale, unmarked.

THORAX.— Pronotum with two pairs of small dark red spots laterally (Fig. 38A). Meso- and metanota pale, unmarked. **Wings**: Venation green, except for certain crossveins. Fore wing length 13 mm; costal crossveins 4–10, origin of Rs, R-Rs crossveins, Psm-Psc crossveins 1–3, cubital and

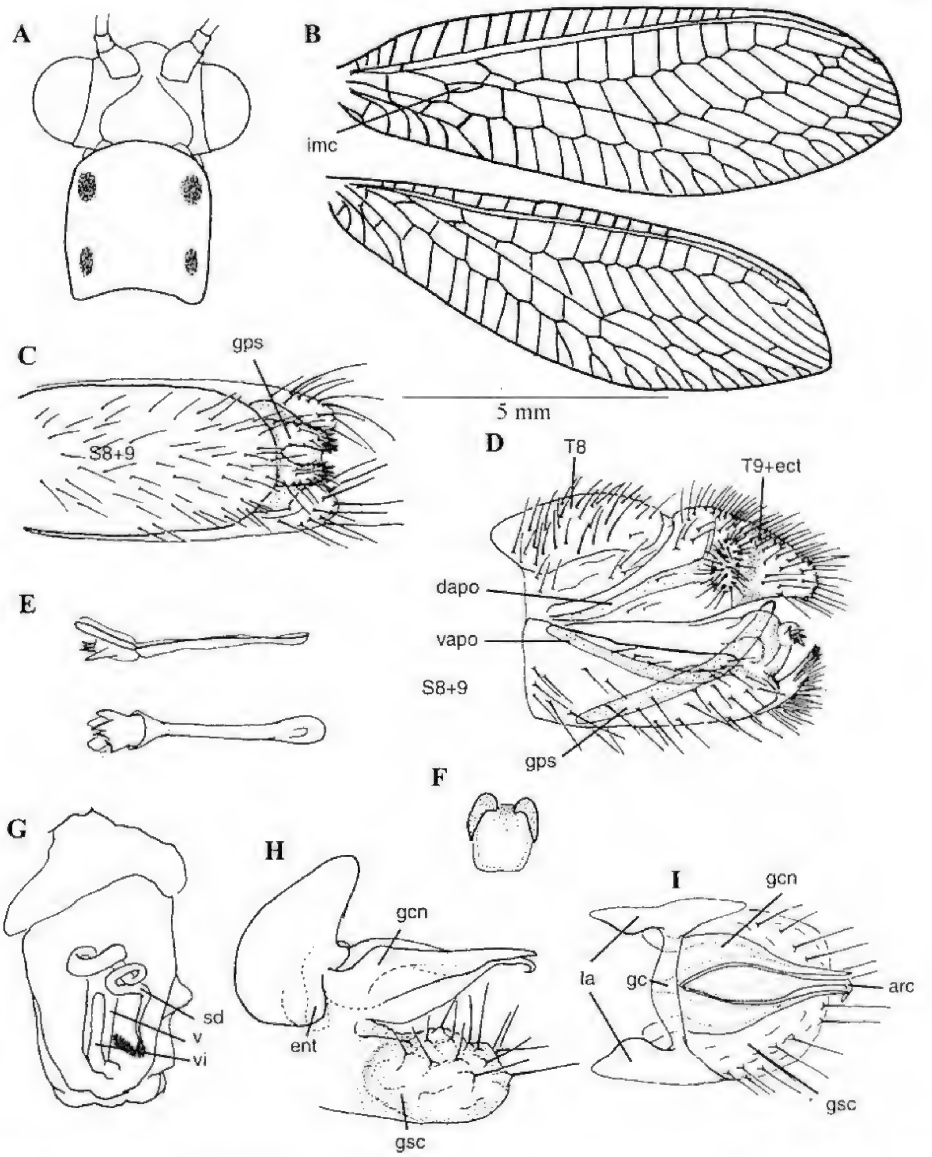


FIGURE 38. *Ceraeochrysa paraguaria* (Navás, 1920). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, ventral view; D. Male abdomen apex, lateral view; E. Gonapsis. F. Subgenitale; G. Spermatheca; H. Male genitalia, lateral view; I. Male genitalia, dorsal view.

anal veins, imc crossvein, inner and outer gradates dark (Fig. 38B). hindwing costal crossveins dark.

ABDOMEN.— Green, unmarked. **Male**: Tergite IX + ectoprocts deeply divided dorsally to form two separate lobes (Fig. 38D). Sternite VIII + IX apically bifurcate (Fig. 38C). Gonarcus narrow, lateral arms projected vertically. Entoprocessus short and wide; gonocornua long, tapered, extended to apex of arcessus (Fig. 38H, I). Arcessus triangular, apically strongly decurved. Gonosaccus with many long setae. Gonapsis slender with multi-pronged apical appendage (Fig. 38E). **Female**: Subgenitale short and wide (Fig. 38F); spermatheca short and thick, with twice-coiled spermathecal gland (Fig. 38G).

HOLOTYPE ♀.— **PARAGUAY**: Rio Paraguay, February 1920 (MNHN).

MATERIAL EXAMINED.— **PARAGUAY**: Rio Paraguay, February 1920 (♀-type)(MNHN); **BRAZIL: São Paulo**, Taquaritinga, 7 January 1993, S. Freitas (9♂♂, 12♀♀-SFC); Jaboticabal, 17 February 1995, S. Freitas (12♂♂-SFC); 20 October 1994, A. Chagas (2♀♀-SFC).

GEOGRAPHICAL DISTRIBUTION.— Paraguay, Brazil.

SPECIES RELATIONSHIPS.— This species is recognized by the four small round spots on the pronotum. Sometimes *C. paraguaria* is confused with *Plesiochrysa brasiliensis* when only external morphological characteristics are considered. However, *Plesiochrysa brasiliensis* is a larger, more robust species, with pronotum that is longer than wide. The pronotal marks of *C. paraguaria* are much darker and well delimited, not diffuse, as in some other *Ceraeochrysa* species. The male has two small lobes and gonocristae at the apex of sternite VIII + IX, similar to *C. cubana*, but the latter species has a striped pronotum, rugose vertex, and giant abdominal spiracles. *Ceraeochrysa paraguaria* does not appear to be closely related to any of the other species with spotted pronota.

Ceraeochrysa parvula (Banks, 1903) new status

Ceraeochrysa columbiana (Banks, 1903) (No locality, type deposited in MCZ)

DIAGNOSIS.— This species has a black flagellum for at least the first 12 flagellomeres, a lateral black stripe on scape, black gena, lateral dark stripe on pronotum, and wings with dark borders to crossveins. It is similar to *C. lineaticornis*, but has a black gena.

HEAD.— Vertex golden yellow without marks. Frons pale, unmarked. Clypeus pale with lateral black stripe (Fig. 39C, D). Maxillary palpi pale or amber. Gena dark red-brown. Antennal scape with dorso-lateral red stripe and a small diffuse red spot on frontal surface; pedicel and first 11 flagellomeres black, more distal flagellomeres progressively more pale fuscous; antennal fossa marked with red.

THORAX.— Pronotum with lateral red stripe (Fig. 39A,C); cervical sclerites red; meso- and metanotum pale, unmarked. **Wings**: Fore wing length 11 mm, longitudinal veins green, transverse veins slightly darkly bordered (Fig. 39B). Hindwing length 9 mm; costal, radial, and gradate crossveins black.

ABDOMEN.— **Male**: Dorsal apodeme of ectoproct bifurcate and ventral branch caudally projected (Fig. 39E). Gonarcal medial arch stout, anterior margin highly curved; gonocornua with acute apex and ventral projection (Fig. 39F, G); narrow arcessus, apical plate trilobed, the medial point horn-like, no dorsal processes; gonosaccus with a field of long setae (Fig. 39I)). Gonapsis apically forked (Fig. 39H).

HOLOTYPE ♂.— **U.S.A.**: **Florida**, Osceola Co., Runnymede, 28°16′50″N, 81°14′39″W, (reared from cocoon)(MCZ). Images of types of both *A. parvula* and *C. columbiana* available on MCZ website.

MATERIAL EXAMINED.— **U.S.A.: Florida**, Osceola Co., Runnymede (1♂-holotype of

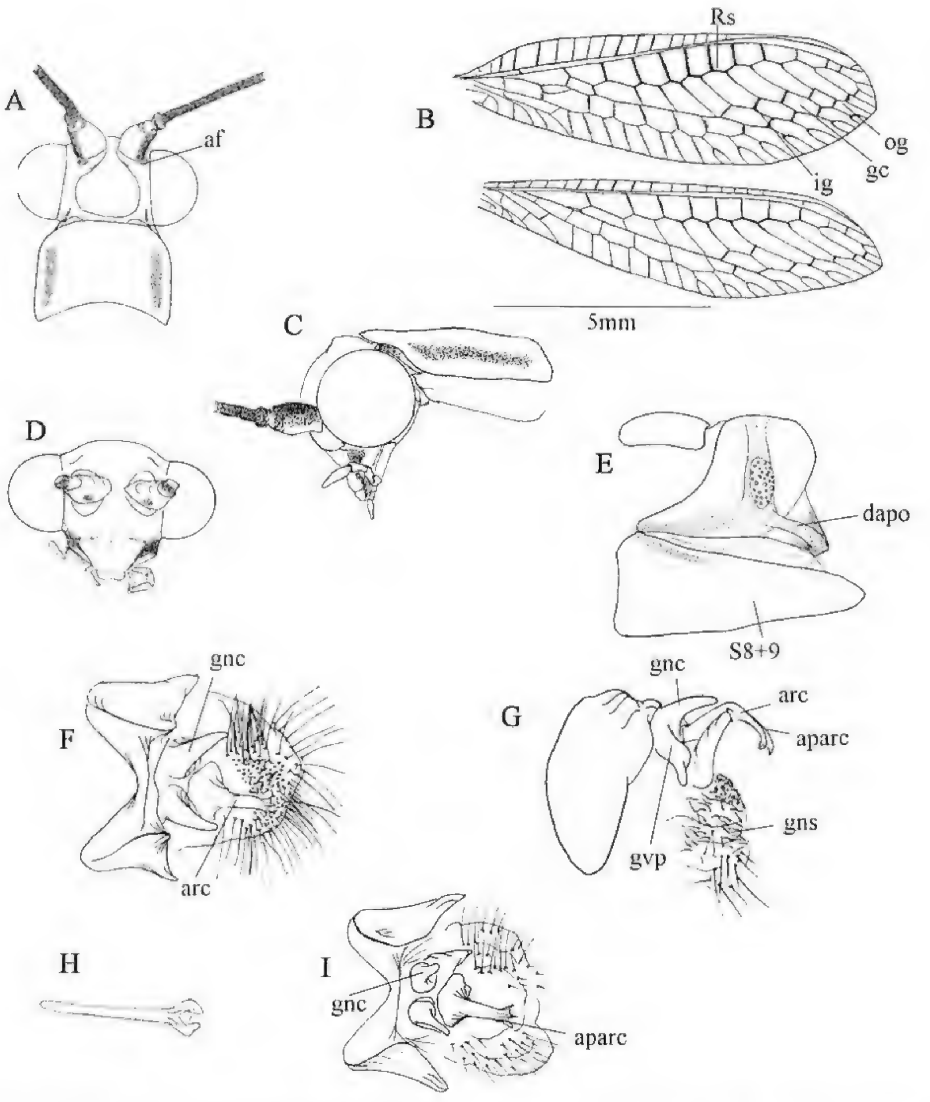


FIGURE 39. *Ceraeochrysa parvula* (Banks, 1903) comb. n. A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, lateral view; D. Head, frontal view; E. Male abdomen apex; F. Male genitalia, dorsal view; G. Male genitalia, lateral view; H. Gonapsis; I. Male genitalia, frontal view.

A. parvula) (MCZ); **D.C.**, Washington (no date), (1♂-holotype of *C. columbiana*)(MCZ); **Honduras**: Siguatepeque, 7 August 1976, P. Adams (1♂-CAS).

GEOGRAPHICAL DISTRIBUTION.— Eastern U.S.A. to Honduras.

SPECIES RELATIONSHIPS.— It is similar to *C. lineaticornis*, but has a black gena.

REMARKS.— see *C. lineaticornis* for remarks on the history of this species. The original choice of names is unfortunate because there is a European species named *Chrysopa parvula* Doumerc, 1861.

***Ceraeochrysa placita* (Banks, 1908)**

Ceraeochrysa intacta (Navás, 1912)(type ?)
Ceraeochrysa forreri (Navás 1914a)(Mexico, type ♂ in BMNH-London)

DIAGNOSIS.— This species has distinctive black marks on the head: dark palpi, dark gena, two dark lines ventrally on frons, and two dark lines on vertex at margin of eyes.

HEAD.— Vertex pale with thin black stripes near the eyes; two suffused small spots in the middle. Frons pale, ventrally bordered by curved black to dark brown spots (Fig. 40C). Gena entirely black (Fig. 40D). Clypeus pale, lateral margins black bordered. Maxillary and labial palpi black dorsally.

THORAX.— Pronotum medially yellow, black marks on lateral margins and indistinct rufous marks submedially (Fig. 40A). Meso- and metanota without distinct marks. **Wings**: Fore wing

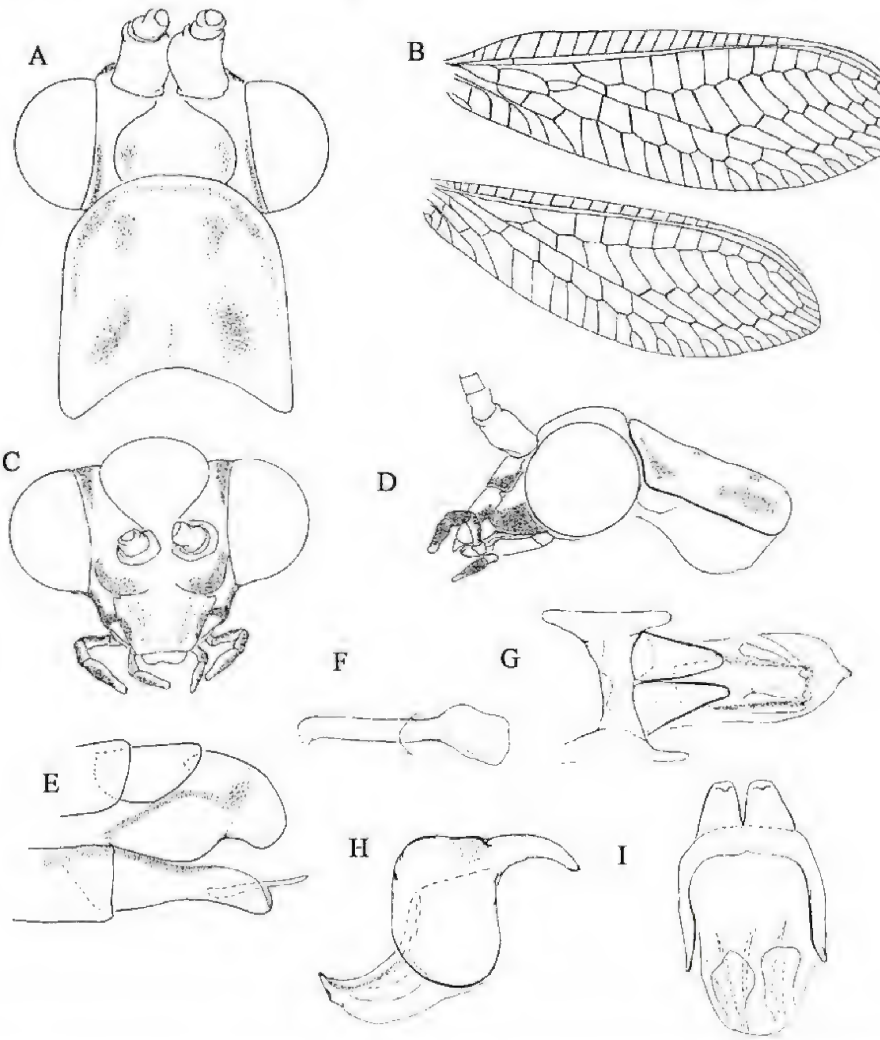


FIGURE 40. *Ceraeochrysa placita* (Banks, 1908). A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Head and prothorax, lateral view; E. Male abdomen apex, lateral view; F. Gonapsis; G. Male genitalia, dorsal view; H. Male genitalia, lateral view; I. Male genitalia, frontal view.

length 14 mm, costal crossveins black, other crossveins black at endings; gradates black (Fig. 40B). hindwing length 13 mm; costal crossveins black, base of Rs black, gradates black.

ABDOMEN.— **Male**: IX tergite expanded laterally (Fig. 40E). Sternite VIII + IX narrow. Gonarcal arch straight, lateral arms rounded, plate-like; gonocornua short and tapered; broad and juxtaposed at base (Fig. 40G,H). Arcessus inside an eversible gonosaccus; median plate curved ventrally (Fig. 40I); membrane of arcessus folded ventrally at apex to form a tooth; gonosaccus opens laterally. Gonapsis long and slender with a plate-like apex, anterior extremity furrowed, dish-like (Fig. 40F).

LECTOTYPE ♂.— **USA: Colorado**, Golden, Chimney Gulch, 39°45′09″N, 105°13′57″W, 20 July 1907, Oslar (MCZ). Images of type available on MCZ website.

MATERIAL EXAMINED.— **USA: Colorado**, Golden, Chimney Gulch, Clear Creek, July, Oslar (2♂♂ lectotype and paralectotype – MCZ); **New Mexico**, Bluewater Lake, 26 July1960, E.S. Ross, (1♀ – CAS).

GEOGRAPHICAL DISTRIBUTION.— USA (Colorado & New Mexico).

SPECIES RELATIONSHIPS.— For many years a species has been identified as *C. placita* that has bright red markings on the head, thorax, and abdomen. However, the syntype series from Colorado is much darker in coloration. To complicate matters even more, the reddish specimens from the northeastern U.S.A. and Canada have somewhat different markings than the populations in the western U.S.A. The reddish line that runs along the top of the gena and above the clypeus, as well as the red line laterally on the vertex tend to be absent, or possibly fade easily in the northeastern population. The thorax has a dorsomedial line that is quite pale, almost white. It is bordered laterally by some reddish coloration that is darkest at mid-length and fades out both anteriorly and posteriorly, to give this border the aspect of a faint pink spot in northeastern specimens. The dark form of *C. placita*, as exemplified by the syntypes, and the reddish form are clearly closely related. The male genitalia of both have a gonarcus with lateral arms that are quite long vertically and gonocornua that are close together and triangular in shape. However, the gonocornua of the dark form are much longer than those of the reddish form. They extend well beyond the lateral arms of the gonarcus. So, we have decided that the reddish form belongs to a separate species, *C. chiricahuae*.

Beyond the clear link between these two species, this sister group shows few relationships to other species within the genus. Tauber (2003) has shown that the larva is quite different than others in the genus. The dark markings on the frons are also found in *C. pseudovaricosa*, but we consider this to more likely be a primitive character state held in common with *Chrysopodes*, and not a synapomorphic state that denotes a close relationship.

Ceraeochrysa pseudovaricosa Penny, 1998

DIAGNOSIS.— This species is distinctive in several respects. It has a small reticulate network of veins in the middle of the inner gradate series. The red spots on the frons are not frequently seen in *Ceraeochrysa*, and the male gonarcus is quite elongate, as is sternite VIII + IX.

HEAD.— Greenish. Vertex raised with two anterior and two posterior dark red spots. Frons pale except for two red spots. Gena brown. Clypeus pale with lateral brown border. Maxillary palpi black. Antennal scape with lateral black stripe and a short black stripe on the dorsal surface; pedicel laterally black; flagellum pale.

THORAX.— Pronotum green with lateral red stripes; mesoscutum marked with red anteriorly. Metascutum marked with red medially. **Wings**: Fore wing length 13 mm; costal area basally wider than usual for *Ceraeochrysa* species; crossvein endings black; intramedian cell with wide base; gradates black; 2nd inner gradate crossvein reticulately branched into various darkened veinlets

with darkly bordered membrane to create a dark spot in the middle of the wing; distal R-Rs crossveins and apical forks darkly bordered; posterior marginal area wider than usual (Fig. 41B). hindwing length 11 mm; venation pale.

ABDOMEN.— **Male**: Tergite IX + ectoproct and sternite VIII + IX slender (Fig. 41A); sternite VIII + IX narrow; dorsal apodeme of ectoproct short. Gonarcal arch narrow with tiny gonocornu as medial tubercles (Fig. 41C–E); arcessus large; median plate very sclerotized posteriorly, apex consists of a medial horn bracketed by lateral prominent lateral folds. Entoprocessus projects caudally. Gonosaccus covered by dense field of small setae and 4–5 long setae on either side. Gonapsis spoon-shaped (Fig. 41F).

HOLOTYPE ♂.— **COSTA RICA: Puntarenas**, La Amistad National Park, 8°54′02″N, 82°48′22″W, 1500 m, 18 February 1991, N.D. Penny (INBio).

MATERIAL EXAMINED.— **COSTA RICA: Puntarenas**, La Amistad Natl. Park, 18 February 1991, N.D. Penny (5♂, 5♀)(holotype, allotype and 8 paratypes)(INBio and CAS).

GEOGRAPHICAL DISTRIBUTION.— Costa Rica.

SPECIES RELATIONSHIPS. —The reticuled series of small, darkened cells in the middle of the inner

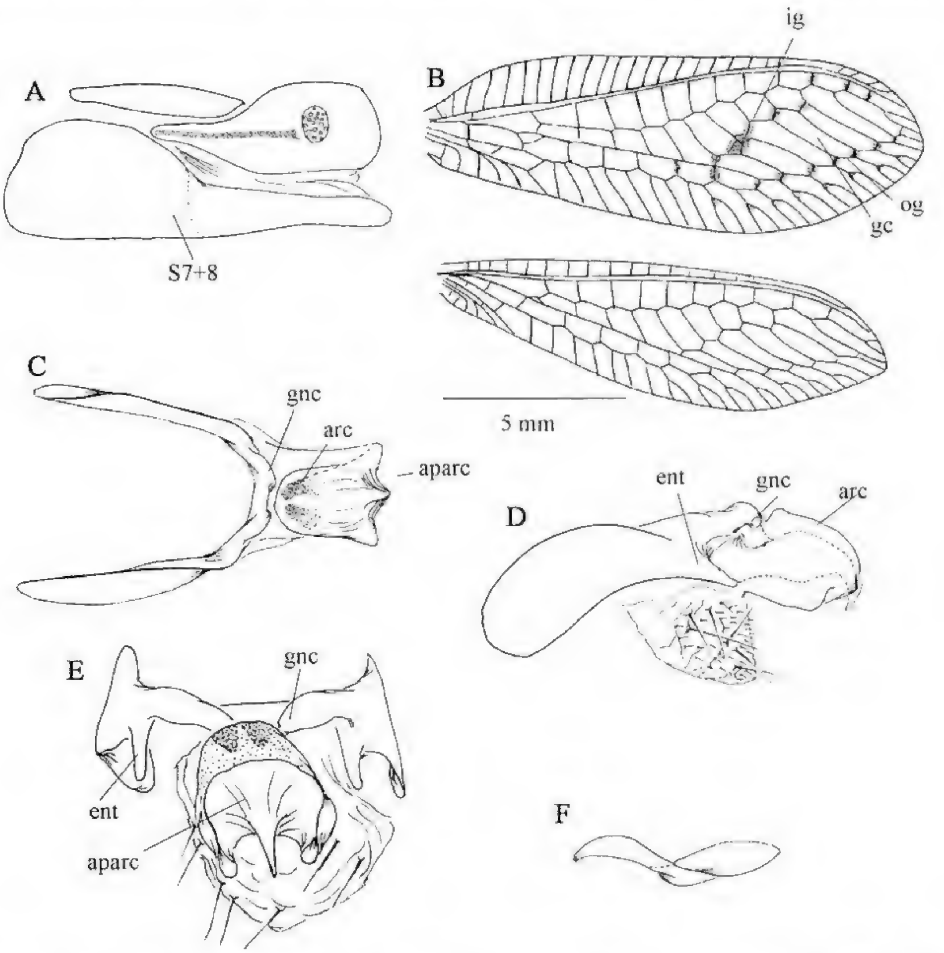


FIGURE 41. *Ceraeochrysa pseudovaricosa* Penny, 1998. A. Male abdomen apex, lateral view; B. Wings; C. Male genitalia, dorsal view; D. Male genitalia, lateral view; E. Male genitalia, frontal view; F. Gonapsis.

gradates series of the fore wing is very similar to the wing of *Chrysopodes varicosa*. However, the two species can be distinguished by the lack of transverse bands on the frons of *C. pseudovaricosa*. The presence of a spoon-shaped gonapsis in the male genitalia indicates its true affinities within *Ceraeochrysa*. However, no other species of *Ceraeochrysa* has this reticulation of the inner gradate series. The generally broad fore wing with broad costal area and reticulate inner gradate series, along with a somewhat shortened gonapsis may indicate a basal position within *Ceraeochrysa* and almost as much in common with *Chrysopodes* as with other members of *Ceraeochrysa*.

***Ceraeochrysa rafaeli* Adams & Penny, 1987**

DIAGNOSIS.— This species shares with several other species the following features: pale antennae, dorsal marks on scape, lateral stripes on pronotum and spots on mesonotum. The features that separate this species are the spermatheca shape and the very sclerotized subgenitale.

HEAD.— Vertex green, unmarked. Frons and genae creamy white, unmarked. Maxillary palpi pale, unmarked. Antennal scape and pedicel with reddish black dorsal stripe not extended into the membranous antennal fossa (Fig.42A); flagellum pale.

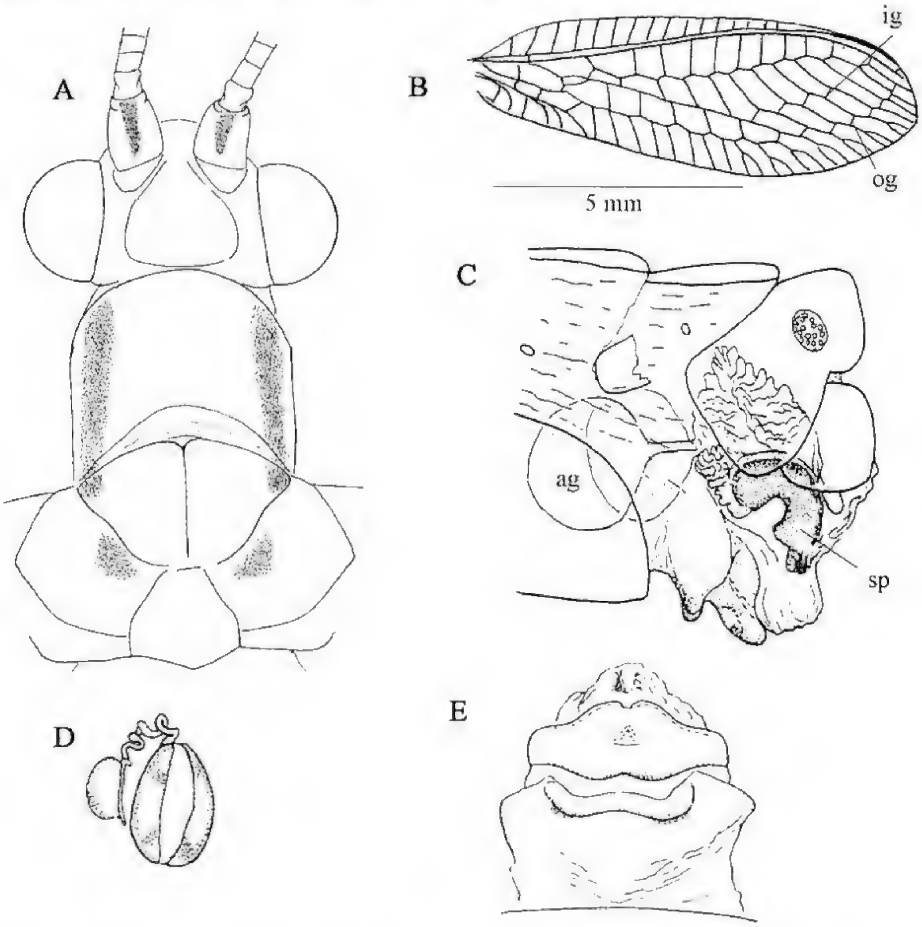


FIGURE 42. *Ceraeochrysa rafaeli* Adams and Penny, 1987. A. Head, pro- and mesothorax, dorsal view; B. Wing; C. Female abdomen apex, lateral view; D. Spermatheca; E. Subgenitale. (Modified from Adams and Penny, 1987).

THORAX.— Bright green. Pronotum with broad reddish black stripe laterally. Mesonotum with two small reddish black spots at anterolateral corners of prescutum and two larger spots more posteromedially on mesoscutum, opposite posterior margin of prescutum (Fig. 42A). **Wings**: Fore wing length 12 mm. Venation green, with many transverse veins darkened: basal costals, R-Rs crossveins, inner (4–5) and outer (7) gradates, most pseudocubitals and posterior marginal forks (Fig. 42B). hindwing Rs dark, the remainder pale.

ABDOMEN.— **Female**: Sternite VII lightly sclerotized with flattened apex. A lingulate, smooth sclerite on membrane of eighth segment, between spiracle 8 and sternite VII (Fig. 42C, E). Subgenitale very broad, caudal lobes confluent with margin laterally; a conical ventromedial pocket opens into a slight depression. Area between subgenitale and sternite VII heavily sclerotized, smooth, projected as a ridge with prominent lateral corners; bursa large; bursal glands open midlaterally, their ducts moderately short; spermatheca elongate, arched dorsally, open to bursa via a wide dorsolongitudinal slit (Fig. 42D); spermatecal duct tightly coiled, ending in a swollen terminal bulb.

HOLOTYPE ♀.— **BRAZIL: Amazonas**: Manaus, 3°01′52″S, 59°56′43″W, 22 June 1982, J.A. Rafael (INPA).

MATERIAL EXAMINED.— see type

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— Without a male, it is difficult to make comparisons. The highly sclerotized subgenitale of the female is distinctive, and what is needed is a series of males associated with females.

Ceraeochrysa reddyi Adams & Penny, 1987

DIAGNOSIS.— Small size. Scape pale, unmarked. Fore wing crossveins all dark. Male apodemes not projected ventrally or caudally. Apex of arcessus with tiny medial tooth and swollen lateral lobes.

HEAD.— Pale, faded, unmarked.

THORAX.— Traces of probable red pronotal stripes, otherwise thorax and legs pale. **Wings**: Fore wing length 10 mm; crossveins completely dark; branches of Rs distal to Psm pale at bases, dark at apex; inner (3) outer (5–6) gradates dark (Fig. 43A). Hindwing venation pale, except costal crossveins and gradates dark.

ABDOMEN.— **Male**: Sternite VIII + IX without projections or modifications. Gonarcus medial arch broad; gonocornua stout (Fig. 43B); small entoprocessus; arcessus elongate, inflated, sharply deflexed apically, tip with dorsal ridge confluent with apical tiny tooth, and subapical lateral expansions on either side

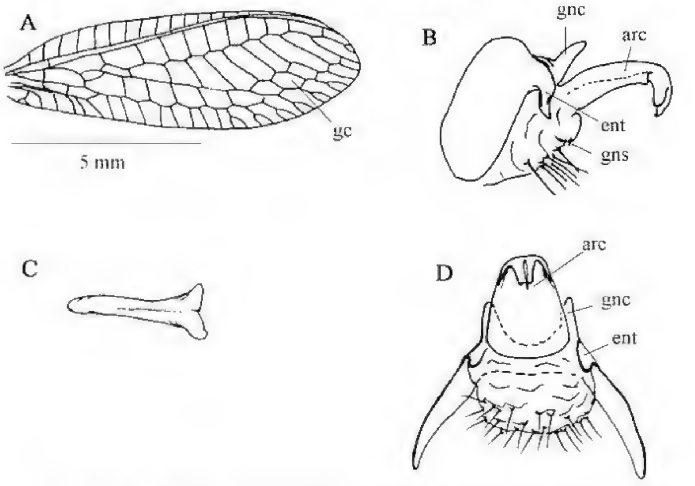


FIGURE 43 (right). *Ceraeochrysa reddyi* Adams and Penny, 1987. A. Wing; B. Male genitalia, lateral view; C. Gonapsis; D. Male genitalia, frontal view. (Modified from Adams and Penny, 1987).

(Fig. 43D); gonosaccus with transverse band of tiny setae above numerous elongate setae on expanded bases. Gonapsis apically forked (Fig. 43C)

HOLOTYPE ♂.— **BRAZIL: Pará**, Serra Norte, 5°52′19″S, 44°56′06″W, August – September 1982, P. Reddy (INPA).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— The male genitalia are structurally similar to *C. parvula*, but the dark head markings of that species are absent. It is possible that *C. reddyi* is a very faded specimen of *C. parvula*, but the latter species has a known distribution considerably north of the locality where the one known specimen of *C. reddyi* was collected.

Ceraeochrysa reducta (Banks, 1944)

DIAGNOSIS.— This species is very poorly known, and is best defined by lack of distinctive features. Males have not been described. There are no marks or spots on the head or antennae; antennae are pale-brownish. The female genitalia have the common features of many *Ceraeochrysa* species.

HEAD.— Pale greenish. Vertex, frons, clypeus, gena and maxillary pale, unmarked. Antennal scape and pedicel pale, unmarked; flagellum pale to fuscous.

THORAX.— Pronotum green with lateral red-orange stripe (Fig. 45A). **Wings**: Fore wing length 14 mm; costal and R-Rs crossveins dark in the middle, gradates inner (3) outer (7) black (Fig. 44B).

ABDOMEN.— **Female**: Spermatheca "U"-shaped, copulatory bursa wrinkled; large sac-like bursal glands (Fig. 44C); area around subgenitale brown, sclerotized (Fig. 44D). Type female is too badly squashed to dissect. Paratype was dissected.

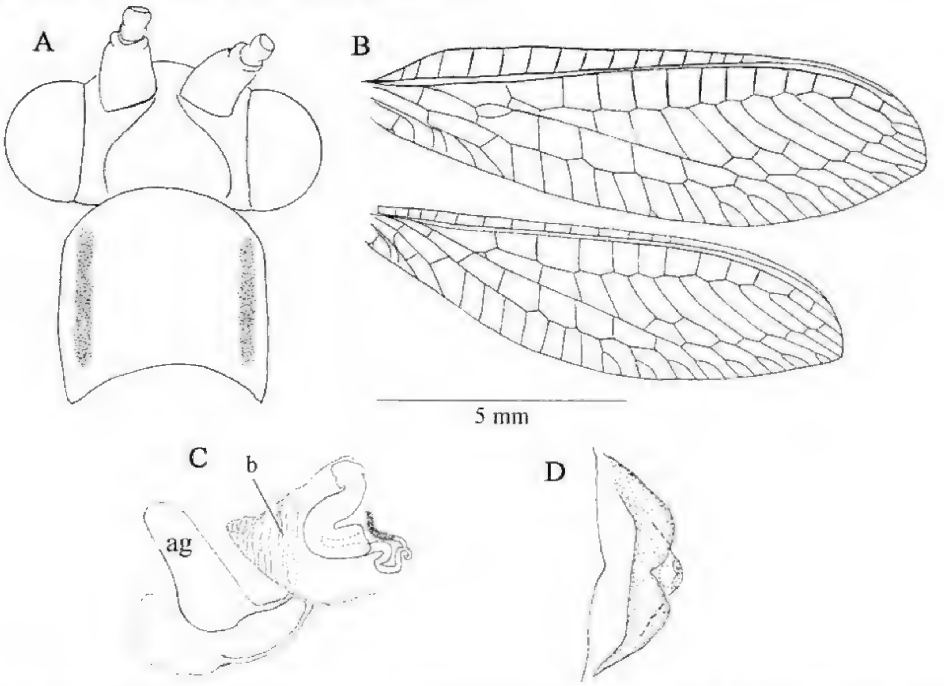


FIGURE 44. *Ceraeochrysa reducta* (Banks, 1944). A. Head and prothorax, dorsal view; B. Wings; C. Female genitalia; D. Subgenitale.

HOLOTYPE ♀.— **COLOMBIA: Boyacá**, Muzo, 5°31′53″N, 74°05′57″W, 900 m, 1936, J. Bequaert (MCZ).

MATERIAL EXAMINED.— **COLOMBIA: Boyaca**, Muzo, 1936, J. Bequaert (1♀ holotype – MCZ); **SURINAM**: Paramaribo, 15 March, Geijskes (1♀ – MCZ).

GEOGRAPHICAL DISTRIBUTION.— Colombia, Surinam.

SPECIES RELATIONSHIPS.— Until this species is better known we can make no comments about phylogeny or relationships.

Ceraeochrysa rochina (Navás, 1915)

DIAGNOSIS.— Head pale, unmarked; antennal scape with dorsal black stripe; pronotum with lateral brown stripes. The dark scape stripe and dark pronotal stripe may be distinctive. Male unknown.

HEAD.— Pale. Vertex, frons, clypeus, gena, and maxillary palpi pale, unmarked. Antennal scape and pedicel pale with dorso-median black stripe (Fig. 45A); flagellum pale.

THORAX.— Pronotum green with brown lateral stripes (Fig. 45A), meso- and metanota pale, unmarked. **Wings**: Fore wing costal crossveins, R-Rs crossveins, base of Rs, cubital crossveins, Psm-Psc crossveins, anals and gradates dark (Fig. 45B); remainder of venation pale.

ABDOMEN.— Female genitalia, spermatheca U-shaped, vela long; bursal gland with long duct (Fig. 45C).

HOLOTYPE ♀ .— **BRAZIL: Ceará**, 1915, (MNHN).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— This species may just be a dark color variant of *C. cincta* or *C. caligata*. We probably won't know until a male from this region with the same color pattern is found.

REMARKS.— The antennae of the type series of *C. rochina* are black, while those of most *C. cincta* are pale. Thus, we find the statement in LeGrand et al. (2009) quite surprising "Both of the specimens (in the MNHN and the MZB) are identical to *Ceraeochrysa cincta* (Schneider,

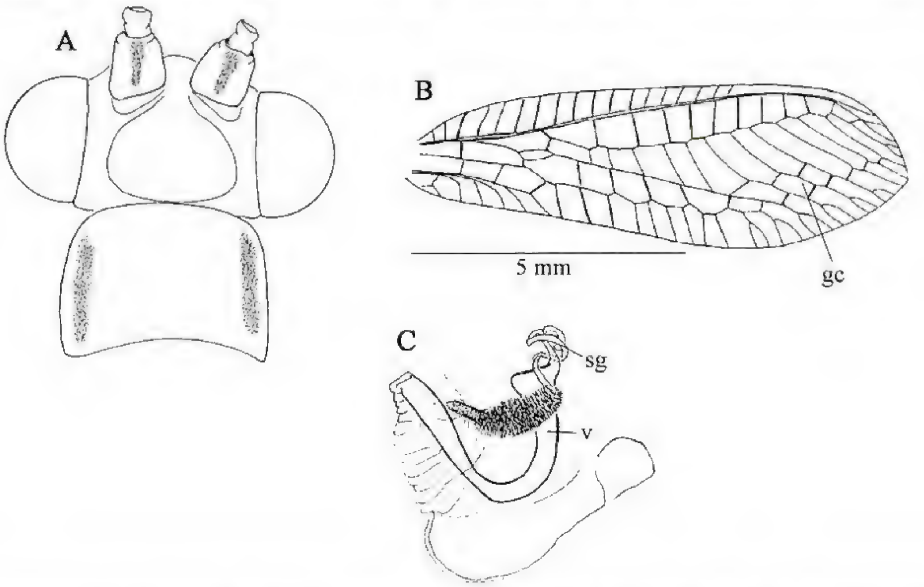


FIGURE 45. *Ceraeochrysa rochina* (Navás, 1915). A. Head and prothorax, dorsal view; B. Wing; C. Spermatheca.

1851), and Navás' illustration in his original description concurs." The Navás illustration referred to does not show the antennae beyond the pedicel. Thus, their subsequent synonymy seems unjustified. There is, however, a population of *Ceraeochrysa cincta* in Florida with black antennae.

***Ceraeochrysa sanchezi* (Navás, 1924e)**

DIAGNOSIS.— This is one of the species with dark antennae which can be separated most easily by characteristics of the male genitalia. The elongate ventral projection of the male ectoproct and subapical dorsal projection of sternite IX are characteristic of this species, as is the pair of triangular fields of gonocristae projecting above and medial to the apex of abdominal sternite IX.

HEAD.— Yellow; frons and gena pale, unmarked; maxillary and labial palpi pale. Vertex pale yellow, rugose, unmarked. Antennal scape and pedicel yellow with lateral brown stripe, continued onto antennal basal membrane (Fig. 46A); flagellum black.

THORAX.— Yellow. Pronotum with broad, lateral, red stripe. Mesopraescutum and mesoscutum with lateral red spots. **Wings**: Fore wing length 11 mm. Venation mostly green with the following crossveins black: costals, origin of Rs, R-Rs; inner and outer gradates, Psm-Psc, anal and cubital vein apices, marginal forks and unforked apices (Fig. 46B). Hindwing costal crossveins 4–10; R-Rs crossveins 5–8; inner and outer gradates dark.

ABDOMEN.— Yellow without marks. **Male**: Tergite IX + ectoproct with digitiform dorsal projection of dorsal apodeme beyond callus cerci and elongate ventral lobe of dorsal apodeme projected ventrally from ectoproct (Fig. 46C); sternite VIII + IX with lateral concavities, which receive ventral projection of ectoproct and subapical dorsally-projected lobes (Fig. 46D). Gonapsis slender, apex with multilobed, spiny appendages (Fig. 46G). Gonarcus medial arch thick, lateral arms triangular in shape (Fig. 46I, J). Entoprocessus quite broad, apically obtusely pointed. Arcessus triangular; apex with medial decurved point. Gonosaccus with three pair of long setae on very enlarged bases. Posterior to gonosaccus a pair of triangular lobes with field of gonocristae. **Female**: Bursa wrinkled, with a pair of large glands (Fig. 46H); spermatheca U-shaped with distal portion dilated (Fig. 46F). Subgenitale with anterior median lobe and posterior sclerotized plate with lateral, rounded lobes (Fig. 46E).

MATURE LARVA. – Intermandibular mark absent; epicranial mark narrow, not extended laterally to edge of cervical margin; head with submedian (postfrontal) mark short, at most extended from midregion of head to antenna; spiracles not on raised tubercles; epicranial and frontal marks linear; postfrontal mark very small and beneath antenna or absent; prothoracic sclerites uncolored to pale amber (Tauber and de Leon 2001).

HOLOTYPE ♂.— **CUBA**: Habana, Playa Chivo, 18 December 1923, Cervera (MCZ).

MATERIAL EXAMINED.— **CUBA**: Habana, Playa Chivo, 18 December 1923, Cervera (♂ – type)(MCZ); **BRAZIL: Rio Grande do Norte**: Assu, 6 June 1991, S. Freitas (2♂♂2♀♀ – SFC); **São Paulo**: Jaboticabal, 5.March.1992, S. Freitas (1♀-SFC); 26 January 1995, S. Freitas (1♂1♀- SFC); **Mato Grosso**: Itiquira, 7 September 1999, S. Freitas (2♂♂, 1♀ – SFC).

GEOGRAPHICAL DISTRIBUTION.— México, Honduras, Brazil, Cuba.

SPECIES RELATIONSHIPS.— This species shares with *C. valida* male genitalia that includes a ventral branch of the dorsal apodeme that projects ventrally to contact a lobe that projects dorsally from the subapical portion of sternite VIII + IX. The gonapsis is also apically expanded and covered with small denticles. Despite these similarities, there are also distinct differences: males of *C. valida* have much narrower gonocornua and its antennae are pale.

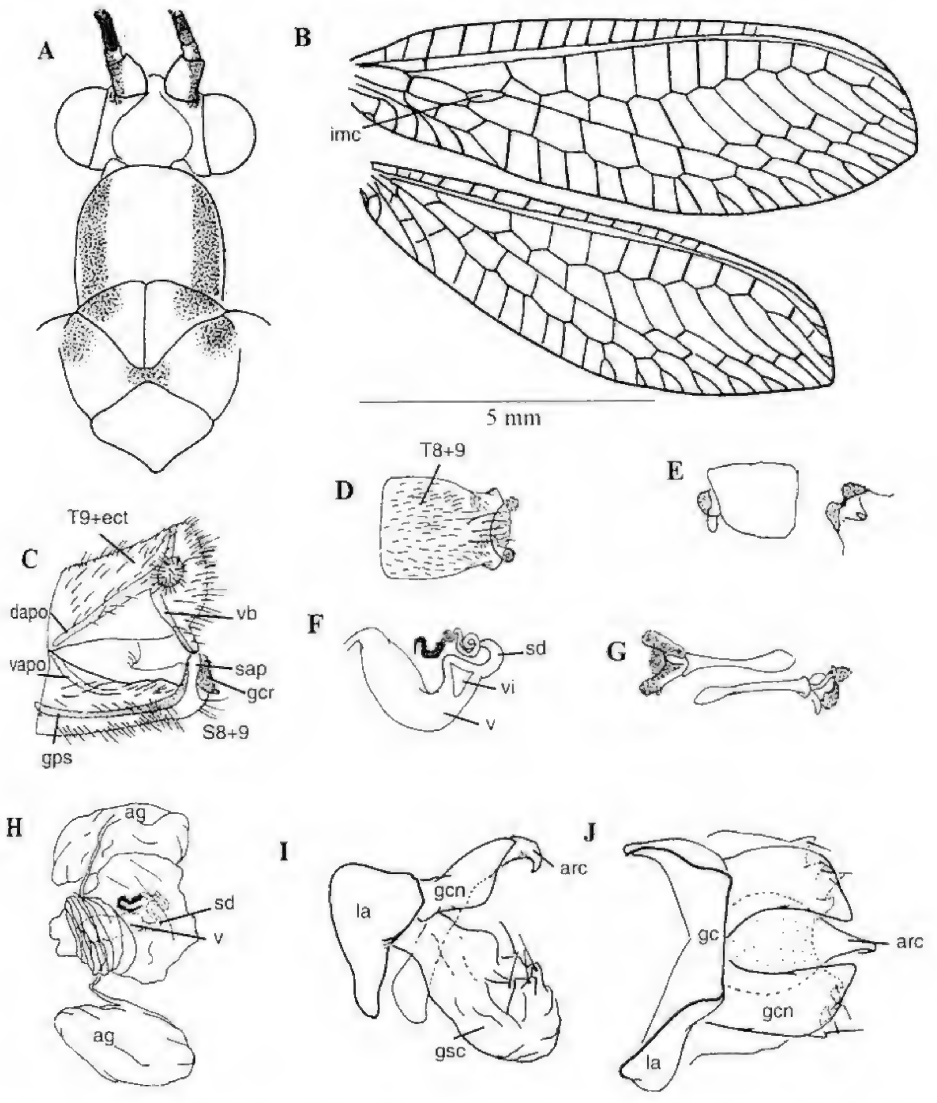


FIGURE 46. *Ceraeochrysa sanchezi* (Navás, 1924a). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex; D. VIII + IX sternites; E. Subgenitale; F. Spermatheca; G. Gonapsis; H. Female genitalia; I. Male genitalia, lateral view; J. Male genitalia, dorsal view.

Ceraeochrysa scapularis (Navás, 1914a)

DIAGNOSIS.— Dark antennae and two dark spots on mesonotum. Male sternite VIII + IX with bifurcate apex with dentate lobe laterally.

HEAD.— Yellowish green. Vertex, frons, clypeus, gena, and maxillary palpi pale, unmarked. Antennal scape with lateral red stripe (Fig. 47A); pedicel dark-ringed; flagellum black.

THORAX.— Pronotum with lateral red stripe (Fig. 47A). Mesonotum with pair of dark red spots. **Wings**: Fore wing length 11 mm. Longitudinal veins green; costal crossveins, origin of Rs, R-Rs crossveins, inner and outer gradates, Psm-Psc crossveins, anals, cubitals, maginal forks, and apices all black (Fig. 47B). Hindwing as in the fore wing: all crossveins black.

ABDOMEN.— Greenish yellow. **Male**: Tergite IX + ectoproct deeply cleft dorsally (Fig. 47C). Apex of sternite VIII + IX with forcipate lobes (Fig. 47D). Gonarcus thick; gonocornua slender and upturned (Fig. 47H, I); arcessus triangle-shaped, apex tapered into a medial point. Gonosaccus with apical field of long setae; posterior to gonosaccus two large lateral lobes with strong gonocristae and medial field of small gonocristae. Gonapsis elongate, narrow, expanded subapically (Fig. 47E). **Female**: Subgenitale, with broad, lateral, rounded lobes; without median projection (Fig. 47G). Bursa with two large glands; spermatheca U-shaped with broad spermathecal duct (Fig. 47F).

HOLOTYPE (no abdomen).— **BRAZIL: Pará:** Santarém, 2°26′03″S, 54°43′00″W, 54/60. (no abdomen)(BMNH).

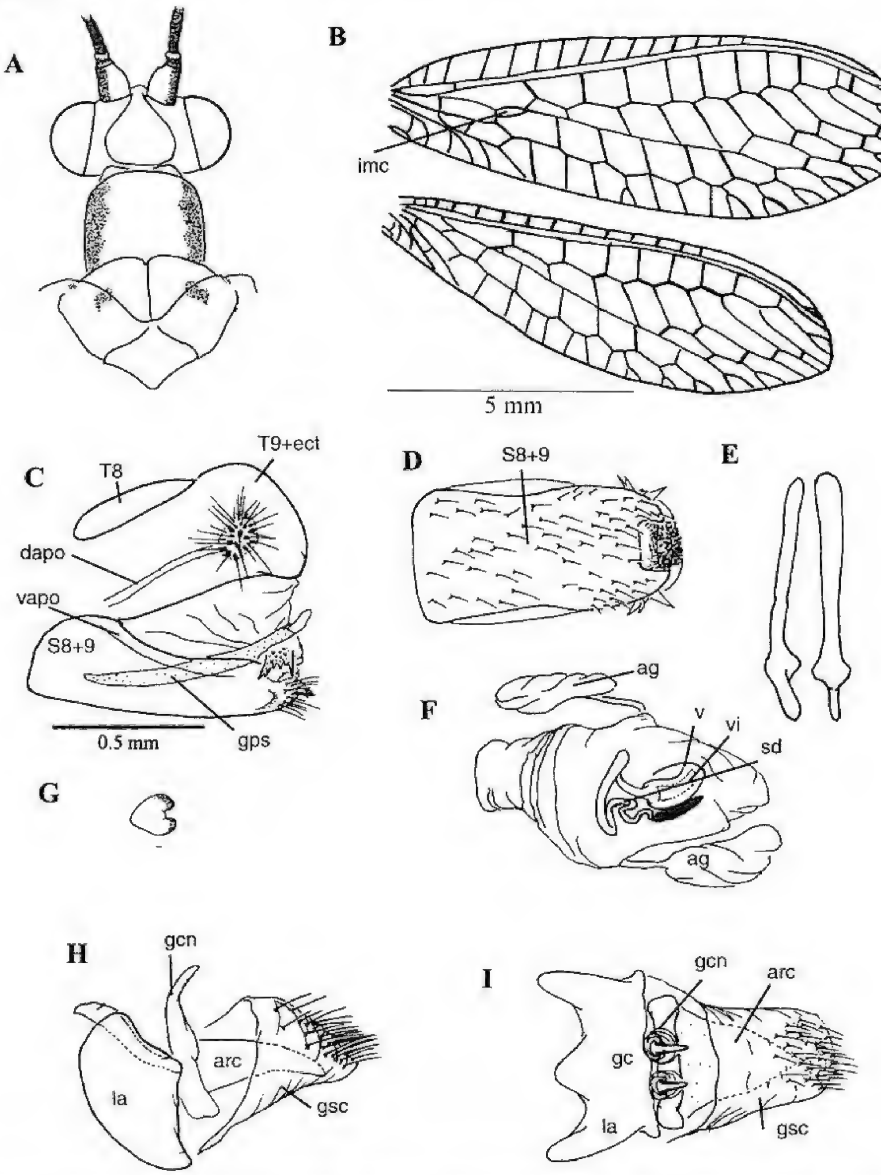


FIGURE 47. *Ceraeochrysa scapularis* (Navás, 1914). A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. VIII + IX sternites; E. Gonapsis; G. Subgenitale; H. Male genitalia, lateral view; I. Male genitalia, dorsal view.

MATERIAL EXAMINED.— **COLOMBIA**: Puerto Wilches, 1984, C.S. Vargas (5♂♂, 11♀♀- CAS, USNM); **BRAZIL: Pará**: Santarém, 54/60. Navás (1? – type)(BMNH); **Roraima**, Boa Vista, 10 July 1977, N.D. Penny, 3♀♀ – INPA); **São Paulo**: Taquaritinga, 8 January 1993, A.L. Xavier (1♂- SFC); Luis Antonio, 8 September 1993, S. Freitas (1♂ – SFC), 21 December 1993, S. Freitas (5♂♂, 3♀♀-SFC).

GEOGRAPHICAL DISTRIBUTION.— Brazil, Colombia.

SPECIES RELATIONSHIPS.— This is a small species most closely related to *C. cubana* and *C. paraguaria*. All three species have a bifurcate apex of male sternite VIII + IX, apical lobes with gonocristae, and chalazate gonosetae. Of the three, *C. scapularis* is the only one with dark antennae and two dark spots on mesonotum.

Ceraeochrysa silvanoi (Navás, 1916)

DIAGNOSIS.— Navás' drawing of the abdomen of this species shows a deeply forked apex of the male sternite VIII + IX. The type itself yields few other clues.

HEAD – Pale, unmarked. Antennal scape, pedicel and flagellum pale.

THORAX.— Pale. Fore wing length 11 mm. Costal and R-Rs crossveins dark; gradates black (Fig. 48A).

ABDOMEN.— **Male**: Sternite VIII + IX forked and extends beyond ectoproct (Fig. 48B, C) (from original description). Type abdomen is now missing.

LECTOTYPE (no abdomen).— **BRAZIL: Rio de Janeiro**: Nova Friburgo, 22°16′58″S, 42°32′04″W, January 1912, Ramos (1? – lectotype)(MNHN). Lectotype designated by LeGrand et al. (2009).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— This species has not been collected since its original description. The type is now in poor condition and the abdomen is gone (LeGrand et al. 2009). The only clue to species relationships is a crude drawing by Navás (reproduced here) of a deeply forked sternite IX. That would tend to align this species with such species as *C. cubana, C. sanchezi*, and *C. scapularis*. Of these, only *C. cubana* has pale antennae. *Ceraeochrysa cubana* has dark stripes on the antennal scape, but they may have faded in this specimen of *C. silvanoi*.

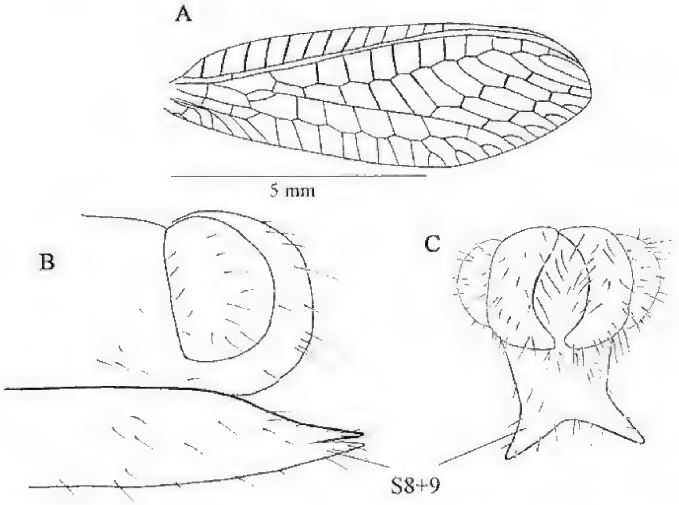


FIGURE 48. *Ceraeochrysa silvanoi* (Navás, 1916). A. Wing. B. Male abdomen apex, lateral view; C. Male abdomen apex, frontal view. (Modified from Navás, 1916).

***Ceraeochrysa smithi* (Navás, 1914a)**

Ceraeochrysa neotropica (Navás, 1929e)(El Salvador and Colombia, types in Hamburg, destroyed)
Ceraeochrysa poeyi (Navás, 1924c)(Cuba, type in MCZ)

DIAGNOSIS.— This striking species has a black base to the antennal flagellum and broad, red, lateral pronotal stripes. However, most distinctive are the red dorsal surface of the antennal scape and the broadly-triangular, red mark on the vertex at the base of each scape. The male also has a subapical dorsal projection on both sides of sternite IX.

HEAD.— Vertex, frons, clypeus, gena, and maxillary palpi pale green, unmarked. Antennal scape red, pedicel dark ringed; base of flagellum black; antennal fossa red (Fig. 49A, B, C).

THORAX.— Pronotum green with broad, lateral, red stripe (Fig. 49A, D). Meso- and metanota green, unmarked. **Wings**: Fore wing length 14 mm. Costal, R-Rs, Psm-Psc crossveins black; inner (3) outer (7) gradates black; marginal forks black; marginal apices black (Fig. 49C). Hindwing length 12 mm. Costal, R-Rs, Psm-Psc crossveins and gradates black.

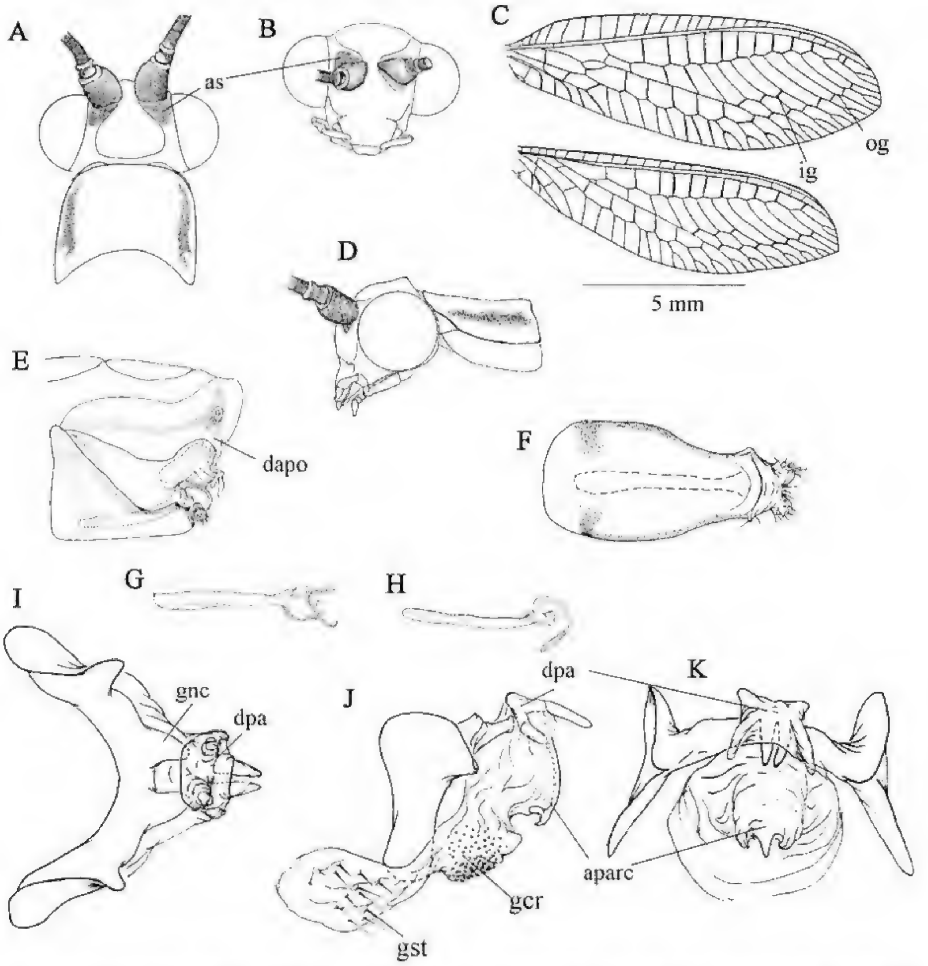


FIGURE 49. *Ceraeochrysa smithi* (Navás, 1914a). A. Head and prothorax, dorsal view; B. Head, frontal view; C. Wings; D. Head and prothorax, lateral view; E. Male abdomen apex, lateral view; F. VIII + IX sternites, ventral view; G. Gonapsis, dorsal view; H. Gonapsis, lateral view; I. Male genitalia, dorsal view; J. Male genitalia, lateral view; K. Male genitalia, frontal view.

ABDOMEN.— Green, without dark markings. **Male**: Ectoproct ventrally projected apically (Fig. 49E). Ventral apodeme of sternite VIII + IX with bifurcate apex and pair of apical membranous lobes with long setae (Fig. 49F) Gonarcus strongly arched; gonocornua short, obtusely pointed; arcessus with dorsal, horn-like projections and apical plate with median hook (Fig. 49I–K); gonosaccus with field of dense gonocristae and long setae. Gonapsis long, apex with filamentous projection (Fig. 49G, H).

MATURE LARVA.— Intermandibular mark absent; epicranial mark globular, extends laterally to edge of cervical margin; lateral tubercles on abdominal segments 2–7 marked with brown; frontal marks broad, joined by pale brown area medially; genal mark extends ventrally to base of maxillae; distal segment of labial palp brown; pronotal plates brown throughout (Tauber and de Leon 2001).

HOLOTYPE ♂.— **Windward Islands (West Indies): GRENADINES**, Union, 13°00′48″N, 61°13′49″W, W.J.H.H. Smith (BMNH).

MATERIAL EXAMINED.— **USA: Florida**, Highlands Co, Archibold Biological Station, 13 October 1964, P.H. Arnaud, Jr. (1♀-CAS); Sebring, 26 October 1956, M.H. Muma and H.L.G., (1♂-CAS); Highland Hammock State Park, 23 January, 1986, T. Eisner (1?-CUIC); 20 April 1987 (1? – CUIC); 22–29 March 1989 (2 ? – CUIC); Indian River Co., Vero Beach, 19 January 1989, T. Eisner, (2? – CUIC); Miami-Dade Co., Biscayne Bay, Mrs. A.T. Slosson, (1♀-AMNH); Orange Co., Orlando, April 1910, F.R. Cole, (1 ?-USNM); Pinellas Co., Palm Harbor, 26 October1956, M.H. Muma (1♂-CAS), 13 May 57 (1♂1♀- CAS); Polk Co., Lake Alfred, M.J. and C.A. Tauber, 2♂♂, 3♀♀, 1?-CAT); Sarasota Co, Sarasota, 5 September 1958, E. MacLeod (2♂♂- CAS); Sumter Co., Bamboo, December 1949, A. DeBach, (1♀-UCR); **MEXICO: Baja California Sur**, Isla San Jose, Punta Ostiones, 8–9 April 1974, J.T. Doyen, (1? – CAS); **Coahuila**, 12 mi N Hermanas, 11 August 1959, L.A. Stange and A.S. Menke (1♂-FSCA); **Veracruz**, 20 mi S. Pernuco, 14 August 1959, L.A. Stange and A.S. Menke (1♂-FSCA); **HONDURAS: Cortes**, Peña Blanca, 23 June–14 July1980, P.A. Adams (2♂♂, 7♀♀-CAS); 19–30 June.1980, P.A. Adams (2♂♂5♀♀ – CAS); 1 km E Varal, 22 July 1968, P. Adams (1♀- CAS); La Lima, 30 June–1 July 1980, P.A. Adams (2♂♂-CAS); **COSTA RICA: Guanacaste**, Finca La Pacifica, 11 February 1969, J.K. Sheldon (4♂♂, 1♀ – CAS); **WINDWARD ISLANDS** (West Indies): Grenadines, Union, W.J.H.H. Smith (1♂ – holotype)(BMNH).

GEOGRAPHICAL DISTRIBUTION.— USA, Cuba, Mexico, Guatemala, Honduras, Costa Rica, and Grenadines.

SPECIES RELATIONSHIPS.— This species shares with *C. michaelmuris* and *C. paraguaria* a pair of spinous lobes above the apex of the sternite VIII + IX in males, although these lobes are not as well developed in *C. smithi*. The most distinctive features are the bright red antennal scape and antennal fossa on the vertex. The only other species with red pigmentation that fills the antennal fossa dorsally is *C. belizensis*, which does not have as extensive red pigmentation on the scape and does not have the subapical dorsal projection of the male sternite VIII + IX.

***Ceraeochrysa squalidens* Adams & Penny, 1987.**

DIAGNOSIS.— This species has no distinctive marks on head, thorax and abdomen, but the apex of the male sternite VIII + IX has a lingulate projection from each posterolateral corner with setae that have thickened, cone-shaped bases. The medial arch of the gonarcus bears a bilobed, vertical, dorsal hood. The gonapsis is apically forked into a dorsal brush and ventral coiled filament.

HEAD.— Vertex, frons, clypeus, gena and palpi pale, unmarked. Antenna pale; scape and pedicel unmarked; flagellum dark amber.

THORAX.— Pronotum green with red stripe laterally from the anterior to posterior margin; meso- and metanota green. **Wings**: Fore wing length 12 mm; venation pale green with crossveins dark in costal, radial, pseudomedial, pseudocubital areas, and marginal forks. Inner (4) outer (7)

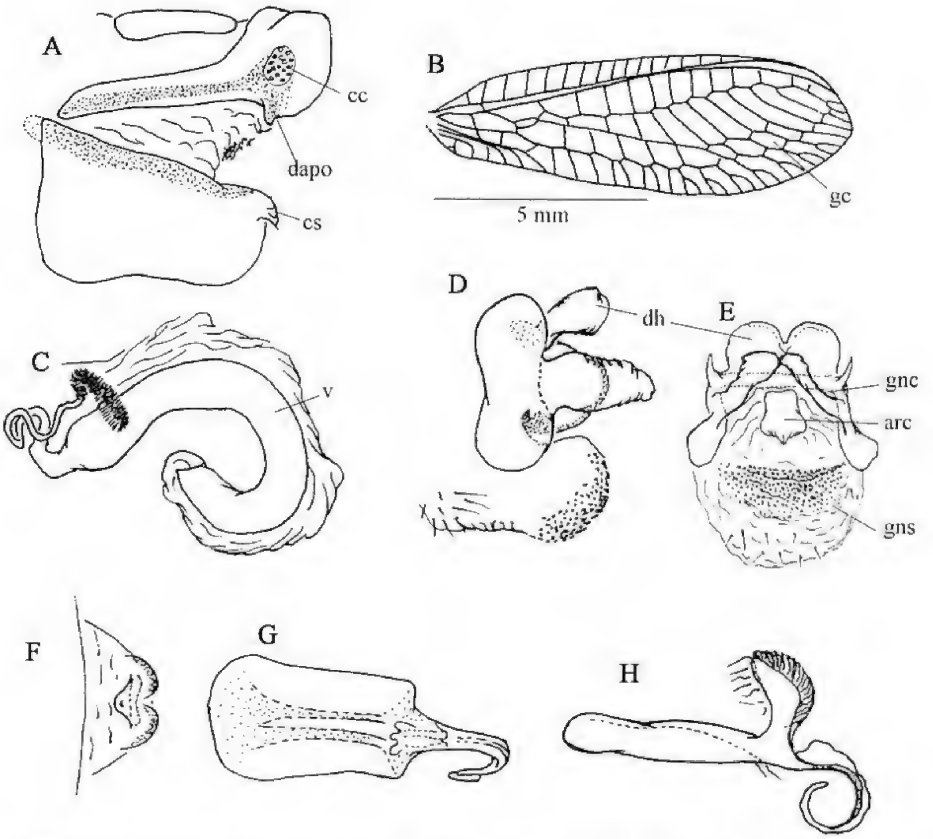


FIGURE 50. *Ceraeochrysa squalidens* Adams and Penny, 1987. A. Male abdomen apex, lateral view; B. Wing; C. Spermatheca; D. Male genitalia, lateral view; E. Male genitalia, frontal view; F. Subgenitale; G. Gonapsis ventral view; H. Gonapsis, lateral view. (Modified from Adams and Penny, 1987).

gradates very dark, without dark borders; series parallel (Fig. 50B). hindwing venation pale. Gradates and radial sector brownish.

ABDOMEN.— Bright green. **Male**: Dorsal apodeme of tergite IX + ectoproct with ventral point (Fig. 50A). Sternite VIII + IX rotund apically, with lingulate projection from posterolateral corner bearing conical-based setae. Gonapsis broad, apicallly with ventral coiled filament in membranous sheath, and dorsally erect, double crest that bears apressed scales (Fig. 50G, H). Gonarcus lateral arms small, medial arch straight; bearing dorsal bilobed vertical plate-like expansion, and diagonal, slightly rugose plates fused medially above arcessus (Fig. 50D, E). Arcessus quadrate, ventral aspect of apex with median hook and lateral tubercles. Lateral to gonarcus an elongate field of small, closely-spaced lanceolate gonocristae. Gonosaccus dorsally with obtusely pointed gonocristae, about as wide as long; ventrally with sparce gonosetae. **Female**: Margin of sternite VII with very pronounced acute projection. Subgenitale with conspicuously projected medial lobe (Fig. 50F) broadly confluent with weakly sclerotized base. Membrane at margin of sternite VII deeply infolded. Copulatory bursa broad; bursal glands round; spermatheca elongate, apex strongly curved; spermathecal duct short (Fig. 50C).

HOLOTYPE ♂.— **BRAZIL: Amazonas**, Manaus, 3°03′02″S, 59°56′36″W, 16 November 1977, N.D. Penny (INPA).

MATERIAL EXAMINED.— **BRAZIL: Amazonas**, Manaus, 16 November1977, N.D. Penny (1♂- holotype)(INPA); 3 June1983, P. Celestino (1♂, 1♀-INPA), 22 June1977, N. Paraluppi, (1♀-INPA).

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— This is one of four species with a broad dorsal hood of the male gonarcus. It shares with *C. dislepis* a medial cleft to this hood, but can be separated from this species by the paler antennae and coiled apex of the gonapsis.

Ceraeochrysa squamma Freitas and Penny 2001

DIAGNOSIS.— This species is a member of the *everes* group with dark antennal flagellum, red lateral pronotal stripes, male gonarcus with dorsal hood and swollen gonocornu.

HEAD.— Vertex, frons, clypeus and gena yellow, unmarked. Maxillary and labial palpi pale. Antennal scape golden yellow, with small brown spot at apical dorso-lateral margin (Fig. 51A); pedicel with lateral brown stripe; flagellum black.

THORAX.— Pronotum green with lateral dark red stripe (Fig. 51A). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 13 mm; venation mostly green with some transverse veins darkened, such as costal crossveins and R-Rs crossveins. Inner (3) and outer (7) gradate series parallel and pale (Fig. 51B). Hindwing venation green, except for dark gradate crossveins.

ABDOMEN.— Green, unmarked. **Male**: Dorsal apodeme of tergite IX + ectoproct strongly sclerotized and with ventral projection (Fig. 51E). Gonapsis flattened, apex recurved as vertical plate-like lobe without teeth (Fig. 51G). Gonarcus medial arch strongly curved, with median, vertical, dorsal hood as long as wide; two inflated dorsolateral gonocornua projected posteriorly from gonarcus (Fig. 51D, H). Arcessus membranous basally; gonosaccus large with dense central field of small stout setae. Plate of randomly organized, pointed scales laterally on membranous wall of genital atrium, probably juxtaposed with ventral projection of ectoproct when depressed.

HOLOTYPE ♂.— **BRAZIL: São Paulo:** Jaboticabal, 20 January 1995, S. Freitas (MZUSP).

MATERIAL EXAMINED.— **BRAZIL: São Paulo:** Jaboticabal, 20 January 1995, S. Freitas, (1♂ – holotype)(MZUSP); 30 September 1977, S. Freitas, (1♂-SFC). 24 April 1999, K. Takahashi (1♂-SFC).

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— The lateral arms of the gonapsis relate this species with *C. costaricensis* Penny, 1997, but it differs in having dark antennae and red stripes rather than spots laterally on the pronotum. The broad, dorsal hood of the male gonarcus is a trait shared with three other species (*C. dislepis*, *C. everes*, and *C. squalidens*), but only *C. everes* and *C. squamma* don't have a medial cleft to that hood. These two species also have a field of scales on the membrane below the male ectoproct. They differ in that *C. everes* has very inflated gonocornua and a much simpler shaped gonapsis.

Ceraeochrysa tauberae Penny, 1997

DIAGNOSIS.— Head pale; pronotum with small dark marks at posterolateral corners; fore wings with darkened fork on dcc and a2–a3 crossvein. Male arcessus with single, elongate, medial lobe; lateral lobes not developed.

HEAD.— Vertex, frons, clypeus, gena and palpi yellow. Anennal scape and pedicel pale without marks.

THORAX.— Pronotum with a faint indication of darker markings at posterolateral corners (Fig. 52A). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 10 mm. Longitudinal veins pale green, crossveins and apical forks brown. The inner (3) and outer (4) gradate series dark brown with extensive infuscation of membrane adjacent to veins. Two additional areas of fore wing

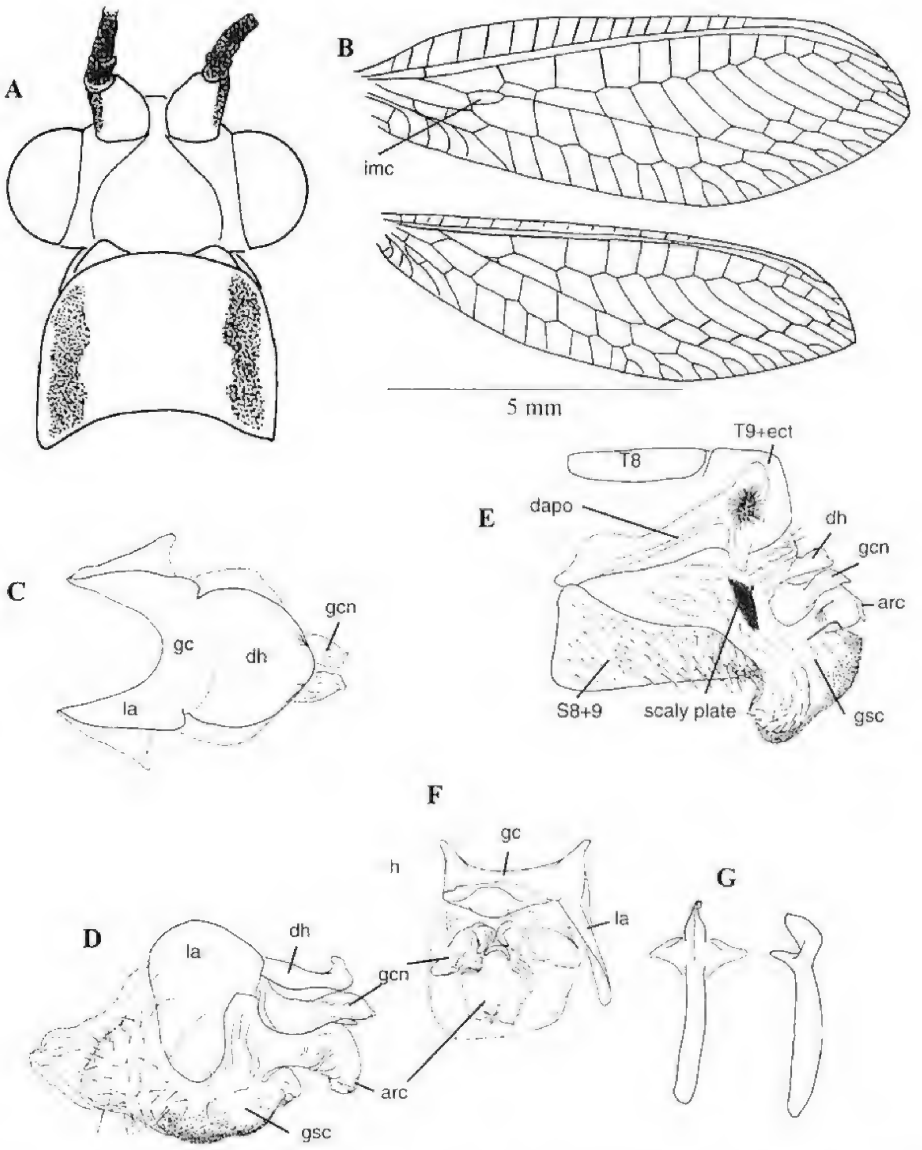


FIGURE 51. *Ceraeochrysa squamma* Freitas and Penny, 2001. A. Head and prothorax, dorsal view; B. Wings; C. Male genitalia, dorsal view; D. Male genitalia, lateral view; E. Male abdomen apex, lateral view; F. Male genitalia, frontal view; G. Gonapsis, dorsal and lateral view.

heavily infuscated: apex of CuP and adjacent crossveins, and 2A-3A crossvein (Fig. 52B). hindwing venation pale.

ABDOMEN.— Green, without dark marks. **Male**: Tergite IX + ectoproct short, only slightly extended ventrally, with scattered chalazate setae; dorsal apodeme apically forked anterior to callus cerci, but without ventral projected lobe (Fig. 52C). Sternite IX elongate, notably narrowed at mid-length. Gonarcus formed by two very broad lateral plates which almost fuse ventrally along midline, medial arch only slightly curved (Fig. 52D, E). Entoprocesses poorly developed as short, pointed lobes caudally and tiny points anteriorly. Arcessus elongate, straight, tapered to apical

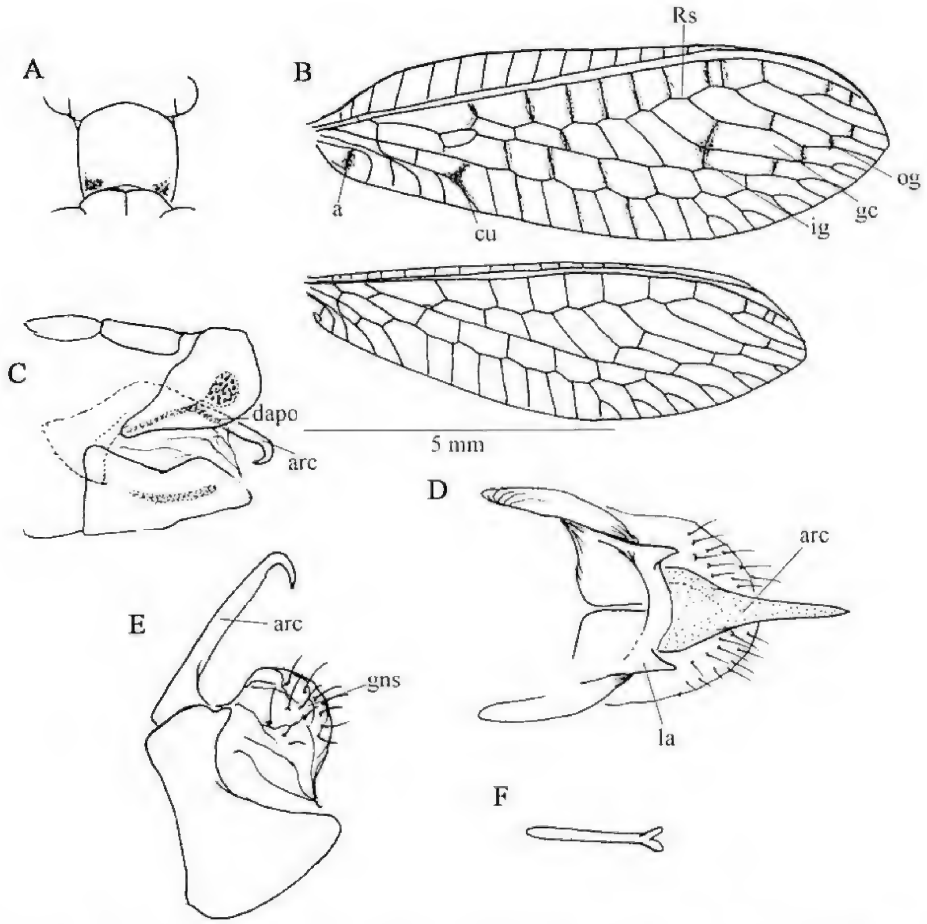


FIGURE 52. *Ceraeochrysa tauberae* Penny, 1997. A. Pronotum; B. Wings; C. Male abdomen apex, lateral view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Gonapsis.

decurved point; gonosaccus with numerous gonosetae. Gonapsis elongate, posteriorly forked, with both forks apically rounded (Fig. 52F).

HOLOTYPE ♂.— **COSTA RICA: Cartago:** near Eslabón, 9°52′57″N, 83°38′27″W, 21 December 1994, C.A. & M. J. Tauber (INBio).

MATERIAL EXAMINED.— **COSTA RICA: Cartago:** near Eslabón, 21 December 1994, C.A. & M.J. Tauber (1♂ – holotype)(INBio); **VENEZUELA: Aragua**, Rancho Grande, 24–31 October, S.S. & W.D. Duckworth (1♀-USNM).

GEOGRAPHICAL DISTRIBUTION.— Costa Rica and Venezuela.

SPECIES RELATIONSHIPS.— This species appears most closely related to *C. nigripedis,* in part due to the long, straight arcessus and shape of the male ectoproct and sternite IX. There is a small dark spot at the lateroposterior margin of the pronotum of both species, and the inner gradate series has a sharp departure from the stairstep series of most species. *Ceraeochrysa tauberae* can be separated from *C. nigripedis* by the lack of dark markings on the meso- and metanota and the lack of dark tarsomeres.

***Ceraeochrysa tenuicornis* Adams & Penny, 1987**

DIAGNOSIS.— This is a small species with margined gradate veins, and a dark brown spot between eye and anterior tentorial pit.

HEAD.— Vertex pale; frons ivory; gena ivory, a dark brown spot between eyes and anterior tentorial pit. Maxillary palpi pale. Antennal scape pale green with a small red mark (Fig. 53A); pedicel and flagellum pale, unmarked.

THORAX.— Pronotum pale green, with broad longitudinal red-brown stripe laterally from anterior to posterior margin (Fig. 53A). Meso- and metanota pale green, unmarked. **Wings**: Fore wing length 9.6 mm. Venation pale, except transverse veins conspicuously darkened. Inner (4) outer (5) gradate series darkly marginated, somewhat irregular (Fig. 53B). Hindwing venation pale green.

ABDOMEN.— Green, unmarked. **Male**: Dorsal apodeme of tergite IX + ectoproct darkly pig-

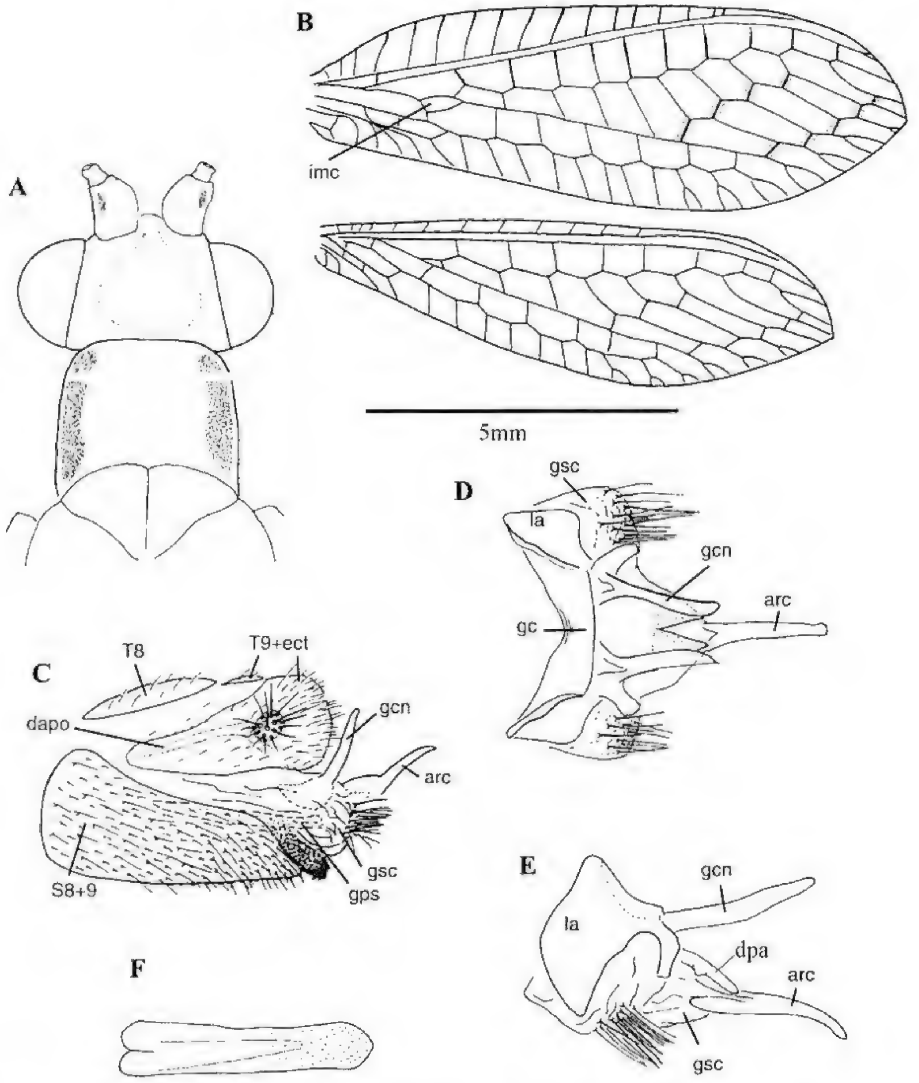


FIGURE 53. *Ceraeochrysa tenuicornis* Adams and Penny, 1987. A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Gonapsis.

mented, not projected ventrally or caudally (Fig. 53C). Sternite IX cleft apically. Lateral arms of gonarcus almost semicircular; medial arch so broad as to become part of lateral arms. Entoprocesses short, vertical. Gonocornua two elongate, slender, dorsocaudal lobes extended more than ¾ length of arcessus. Arcessus divided: into basal sclerite with two short horns, and apical slender sclerite with decurved, acute tip (Fig. 53D, E). Gonosaccus with two groups of long setae laterally; gonocristae large, thorn-like anteromedially, slender laterally. Gonapsis long slender, widened posteriorly (Fig. 53F). **Female**: Sternite VII without obvious modification. Bursa small, triangular, longitudinally wrinkled; bursal glands absent. Spermatheca moderately short, strongly arched. Subgenitale short, wide; with obtuse ventral tip.

HOLOTYPE ♂.— **BRAZIL: Amazonas:** Manaus. 3°03′02″S, 59°56′36″W, 23 April 1976, I.S. Gorayeb (INPA).

MATERIAL EXAMINED.— **BRAZIL: Amazonas:** Manaus. 23 April 1976, I.S. Gorayeb (1♂ – holotype)(INPA), 13 July 1979, J.R. Arias, (1 without abdomen-INPA); 28 Jan. 1981, 29 May 1981, Feb. 1981, 1 Oct. 1981, J.R. Arias, (4♂♂-INPA); **Pará**: Serra Norte, August-September 1982, P. Reddy (2♂♂, 1♀-INPA).

GEOGRAPHICAL DISTRIBUTION.— Brazil.

SPECIES RELATIONSHIPS.— This species is very similar to *C. ariasi*. They both have a dark mark along the dorsal margin of the gena, margined gradate veins, and males have median plate of the mediuneus that tapers to two distal points. The difference between the two species is the relative lengths of the gonocornua, which are much longer in *C. tenuicornis*.

Ceraeochrysa tucumana (Navás, 1919)

DIAGNOSIS.— This is a small species that superficially resembles *Chrysoperla externa* in wing venation, but has dark stripes on the antennal scape and pronotum.

HEAD.— greenish yellow. Frons, gena, and maxillary palpi pale, without dark marks. Antennal scape with lateral brown stripe, pedicel dark-ringed; flagellum pale. Vertex pale green, glabrous, unmarked.

THORAX.— Pale green. Pronotum with lateral, reddish brown stripe (Fig. 54A). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 11 mm Venation mostly green, with costal crossveins, origin of Rs, Rs-Psm, inner (3) outer (5) gradates and Psm-Psc, black (Fig. 54B); hindwing costal crossveins, R-Rs crossveins and gradates black.

ABDOMEN.— Greenish with pale red spots on the tergite II and III. **Male**: Tergite IX + ectoproct deeply divided dorsally to form two lateral lobes (Fig. 54E). Apex of sternite VIII + IX with pointed medial projection and thick-based setae (Fig. 54D). Gonarcus medial arch thick, strongly curved; lateral arms relatively small, triangular. Entoprocesses elongate, thin, decurved. Gonocornua vertically curved, digitiform. Arcessus large, with forked, medio-dorsal horn (Fig. 54I, J); apex upturned as sclerotized lobe with apical hook. Gonapsis elongate, slender rod with apical knob. Gonosaccus with two lateral, swollen fields of long setae (Fig. 54H); between gonosaccus and sternite VIII + IX a membranous area with gonocristae. **Female**: Spermatheca short with thick spermathecal gland (Fig. 54F). Subgenitale with short median projection (Fig. 54G).

HOLOTYPE ♂.— **ARGENTINA: Tucumán**, Tucumán, C.S. Reed (without date) (MLPA).

MATERIAL EXAMINED.— **BRAZIL: São Paulo**: Taquaritinga, 8 January 1993, A.L. Xavier(1♂-SFC); 1 June 1994 R. Narciso, R.(1♀-SFC); Luis Antonio, 8 Sepetember 1993, S. Freitas (1♂-SFC), 21 September 1993, S. Freitas (3♂♂-SFC).

GEOGRAPHICAL DISTRIBUTION.— Argentina, Brazil.

SPECIES RELATIONSHIPS.— The most distinctive feature of this species is the deeply cleft tergite IX + ectoproct, that effectively divides this segment in half. This trait is found to a lesser degree

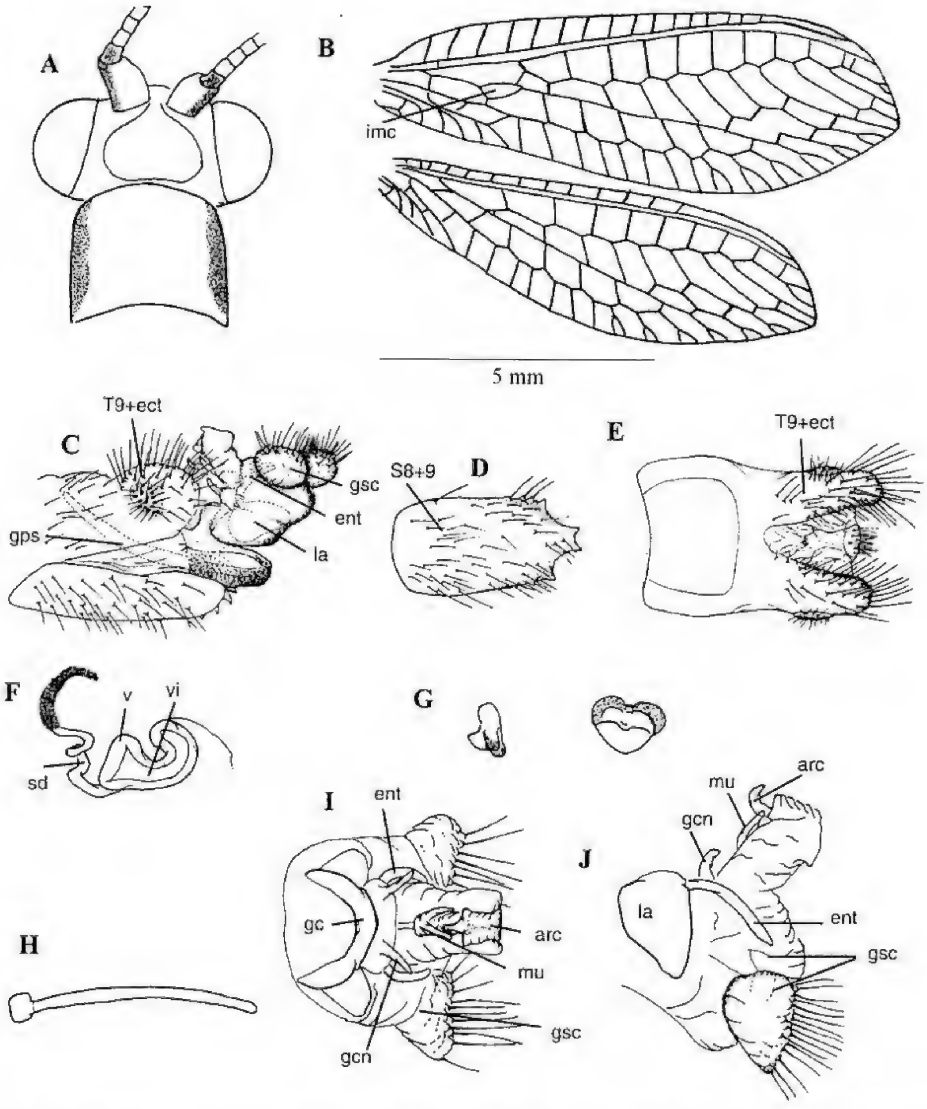


FIGURE 54. *Ceraeochrysa tucumana* (Navás, 1919). A. Head and prothorax, dorsal view; B. wings; C. Male abdomen apex, lateral view; D. VIII + IX sternites; E. Male abdomen apex, dorsal view; F. Spermatheca; G. Subgenitale; H. Gonapsis; I. Male genitalia, dorsal view; J. Male genitalia, lateral view.

in members of the *berlandi* group, but they have dark antennae, a narrow brown pronotal stripe and a mediuncus and arcessus that is triangular and tapered. The greatest similarity is to *C. forcipata* that also has a deeply cleft ectoproct. However, male sternite VIII + IX is much differently shaped, as is the gonapsis. Also, the fore wing of *C. forcipata* has a much longer inner gradate series.

Ceraeochrysa valida (Banks, 1895)

Chrysopa valida Banks, 1895 (Mexico, El Taste, lectotype ♀ in MCZ)
Chrysopa bimaculata McClendon, 1901 (USA, Texas, lectotype ♀ in MCZ)
Chrysopa limitata Navás, 1913a (Brazil, Bri. Guiana, Types in MZBS)
Chrysopa longicella Navás, 1914a (Guatemala, Type ♂ in BMNH)
Chrysopa breviata Banks, 1915 (Ecuador, Type in MCZ)

Chrysopa lioni Navás, 1927 (Haiti, Lectotype ♀ in MNHN)
Chrysopa damiensis Smith, 1931 (Haiti, Type ♂ in MCZ)
Chrysopa wolcotti Smith, 1931 (Haiti, Type ♀ in MCZ)

DIAGNOSIS.— This species has a lateral brown stripe on antennal scape, orange red stripe on pronotum, conical shape of tergite IX + ectoproct. The most distinctive feature of this species is the male dorsal apodeme ventral branch projects ventrally, to often overlap sternite IX; the ventral apodeme has a very prominent subapical dorsal lobe.

HEAD.— green. Vertex, frons, clypeus, and maxillary palpi pale, unmarked. Vertex smooth on female and rugous on male. Antennal scape with a dorsolateral brown stripe (Fig. 55A); flagellum pale.

THORAX.— Pronotum green with orange-red lateral stripe (Fig. 55A). **Wings**: Fore wing length 12 mm; all transverse veins, gradates, marginal forks, and marginal vein apices dark (Fig. 55B, C). Hindwing venation pale, except costal crossveins, anterior ends of R-Rs crossveins and gradates dark.

ABDOMEN.— **Male**: Ectoproct apically pointed. Dorsal apodeme apically branched; ventral branch projected below ectoproct to form ventral point (Fig. 55D). Ventral apodeme forms dorsal,

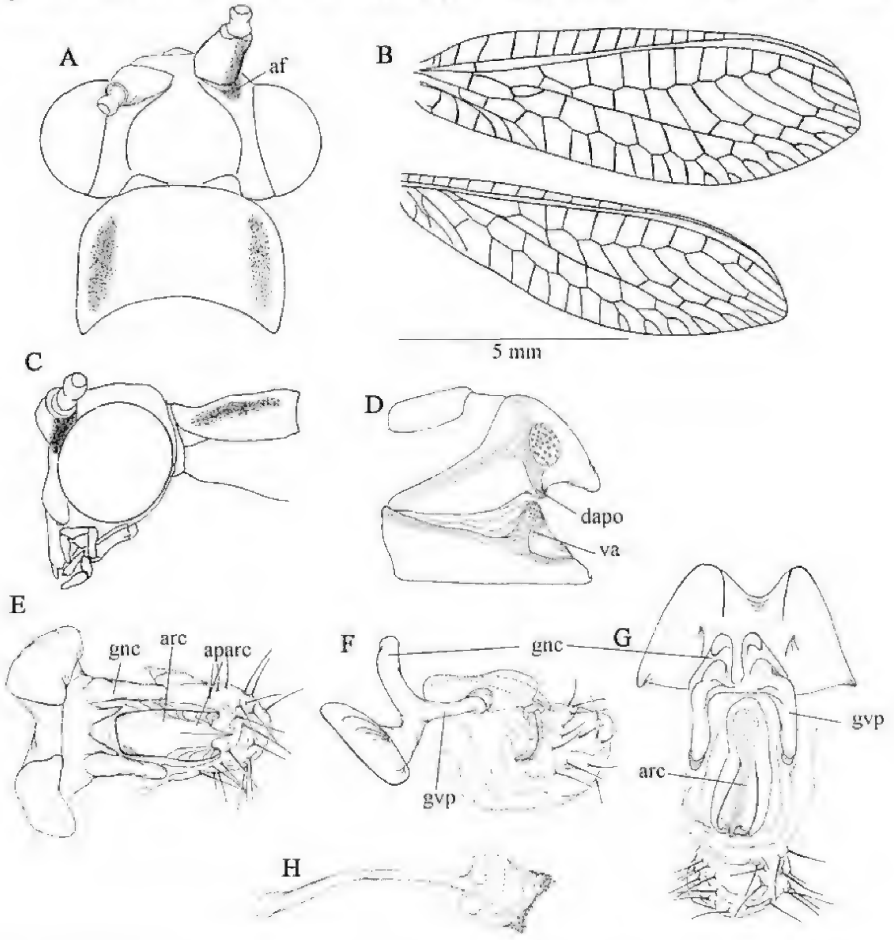


FIGURE 55. *Ceraeochrysa valida* Banks, 1895. A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, lateral view; D. Male abdomen apex, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Male genitalia, Frontal view; H. Gonapsis.

subapical projection of sternite VIII + IX (Fig. 55D). Gonarcal arch very thick and wide; lateral arms small, oval (Fig. 55E). Gonocornua long, tapered to acute point, fused together at base (Fig. 55E, F). Arcessus heavily sclerotized, median plate with apical hook that penetrates deeply into gonosaccus (Fig. 55F, G). Gonosaccus with scattered, long setae. Gonapsis spoon-shaped with apical membranous area that bears a field of little teeth (Fig. 55H).

MATURE LARVA.— Intermandibular mark absent; epicranial mark narrow, not extended laterally to edge of cervical margin; head with submedian (= postfrontal) mark short, at most extended from midregion of head to antenna; spiracles not on raised tubercles; epicranial and frontal marks narrow, but not linear; postfrontal mark distinct, extended from midregion of head to external margin of antenna; prothoracic sclerites brown (Tauber and de Leon 2001).

LECTOTYPE ♀.— **MEXICO**: Baja California Sur, El Taste, 23°26′58″N, 110°04″03″W, September (no year) (MCZ).

MATERIAL EXAMINED.— **USA: Florida**, Brevard Co., Malabar, 4–9 Feb 2001, S. Fullerton et al. (1♂ –CAS); Broward Co., Fort Lauderdale, 8 July 1933, M. Bates (1♂ – MCZ); (county unknown), Pine Island, 4 Jan. 1957, MHM & HLG (1♂ – CAS); **Texas,** Cameron Co. 3 Aug. 1928, L.D. Beamer (1♂ – SEMC); Brownsville, Oct.. 1942, E. Ross (1♀ – CAS); Nov..1942, E.S. Ross, (1♀ – CAS); 2 Oct. 1942, T.E. Burns (1? – CAS); **MEXICO**: Baja **California Sur**, La Paz, 5 Nov. 1961 (1♂ – CMNH); San Jose del Cabo, 14 April 1990, E. Castel & L.H. Williams (2♂♂, 2♀♀ – WFBM); **Jalisco**, Plan de Barrancas, 24 March 1962, F.D. Parker & L.A. Stange (1♂ – CAS); 22 April 1962, F.D. Parker & L.A. Stange (1♂ – CAS); **Oaxaca**, 23 mi s Matias Romero, 7 Aug. 1963, F.D. Parker & L.A. Stange (3♂♂ – CAS); 14 Aug. 1963, F.D. Parker & L.A. Stange (1♂ – CAS); **Veracruz**, Palma Sola, 29 Sept. 1973, Mateu, Herta, Gomez (1♂ – UNAM); **GUATEMALA**: Nueva Concepcion, 17 VIII 63, D.Q. Cavagnaro & M.E. Irwin (1♀ – CAS); **EL SALVADOR**: 6 mi w Quezaltepeque, 12 July 1961, M. E. Irwin (1♀ – CAS); **HONDURAS**: **Cortes**, La Lima, 1 Aug. 1973, P.A. Adams (1♂ – CAS); Peña Blanca, 10 Aug 1976, P.A. Adams (4♀♀ – CAS); San Pedro Sula, 3 Aug. 1973, P.A. Adams (1♂, 1♀ – CAS); **COSTA RICA: Alajuela:** 20 km s Upala, 3–9 March 1991, F.D. Parker (1♂ – EMUS); **Guanacaste**, La Taboga For. Res., 9 km sw Cañas, 11 Feb. 1987, G.E. Bohart (1♂, 1♀ – EMUS); 17–27 Feb. 1987, W.L. Rubnik (3♂♂ – EMUS); 4–6 May 1989, F.D. Parker (1♂, 2♀ – EMUS); 14 km s Cañas, 7–10 Oct. 1989, F.D. Parker (1♂ – EMUS); 14–16 Oct. 1989, F.D. Parker (1♂ – EMUS); 13 Sept. 1990, N.D. Penny (1♀ – CAS), 7–9 Dec. 1990, F.D. Parker (1♂, 1♀ – EMUS; 1♂ – CAS); 12 Feb. – 16 March 1991, F.D. Parker (3♂♂ – EMUS); 24–28 Feb. 1991, F.D. Parker (1♂, 1♀ – CAS); 1–7 March 1991, F.D. Parker (2♂♂ – EMUS); 8–15 March 1991, F.D. Parker (1♂, 4♀ – EMUS); 24–31 March 1991, F.D. Parker (1♂ – EMUS); 5 mi ne Cañas, 25 Dec. 1994, M.J. & C.A. Tauber (3♂♂, 4♀♀ – CMT); 26 Dec. 1994, M.J. & C.A. Tauber (3♂♂, 3♀♀ – CMT); 27 Dec. 1994, M.J. & C.A. Tauber (3♂♂, 3♀♀ – CMT); Finca La Pacifica, 4 Feb. 1969, J.K. Sheldon (5♂♂, 1♀ – CAS); **San Jose**, Escazú, 14–21 Feb. 1988, F.D. Parker (1♂ – EMUS);. **DOMINICAN REPUBLIC**: Santo Domingo, Edgombe, 22 Dec. 1990, A. Abad Autun (1♂, 2♀♀ – CAS). **HAITI**: Damien, 21 Jan. 1930, R.C. Smith (1♂ – SEMC); H. Latham, 28 Jan. 1930, R.C. Smith (1♂ – SEMC); **VENEZUELA: Aragua,** El Limón, 9 March 1970, D. Villasmil & J.C. Marin (1♂, 2♀♀ – MIZA); **Lara**, El Cuji, 7 mi n Barquisimeto, 29 June – 1 July 1967, R.W. Poole (4♂♂, 4♀♀ – CUIC); **Zulia,** Los Hermonitas, 26 June 1979, Brooks & Grigarick (1♂ – UCD); **PERU**: **Laredo**, La Libertad, sand hills e Laredo, 16 July 1982. R.B. Miller & L.A. Stange (1♂, 1♀ – RBMC; 1♀ – CAS); **Piura**, Querecotillo, 25 July 1983, R. B. Miller, L. Stange (1♂, 2♀♀ – RBMC; 1♂, 1♀ – CAS).

GEOGRAPHICAL DISTRIBUTION.— U.S.A., Mexico, Guatemala, Honduras, El Salvador, Costa Rica, Dominican Republic, Haiti, Venezuela, Peru.

SPECIES RELATIONSHIPS.— This is one of two species in which the male ventral apodeme has a dorsal branch that projects above the lateral margin of the sternite VIII + IX: *C. sanchezi* and *C. valida*. Also, males of both species have a dorsal apodeme with elongate ventral branch extended below the ectoproct and a gonapsis with enlarged, toothed apex. However, the two species don't appear to be that closely related. *Ceraeochrysa sanchezi* has black antennal flagellum, male with highly modified apex of male sternite IX, very reduced entoprocesses, and greatly enlarged gonocornua.

REMARKS.— The original description indicates a syntype series from two localities: El Taste and San Jose del Cabo. We herein explicitly restrict the type to the female from El Taste that has the MCZ type label 11995 under it. Also, we are unable to distinguished females from *C. cincta*.

***Ceraeochrysa achillea* Freitas and Penny, sp. nov.**

DIAGNOSIS.— This species has the following features: black flagellum, black stripe on scape; black gena; fore wing with dark and bordered transverse veins; male tergite IX + ectoproct with a caudal spur.

HEAD.— Vetex, frons, clypeus, and maxillary palpi pale, unmarked; gena black (Fig. 56C). Antennal scape and pedicel with dorsolateral black stripe (Fig. 56A); flagellomeres 1–18 black

THORAX.— Pronotum with lateral, brown stripe not well defined. Meso- and metanotum pale, unmarked. **Wings**: Fore wing length 11 mm; costal and Rs crossveins black; inner (4) outer (6) gradates black with dark borders; Psm-Psc crossveins with black borders (Fig. 56B).

ABDOMEN.— **Male**: Tergite IX + ectoproct with small apical spur (Fig. 56D). Dorsal apodeme

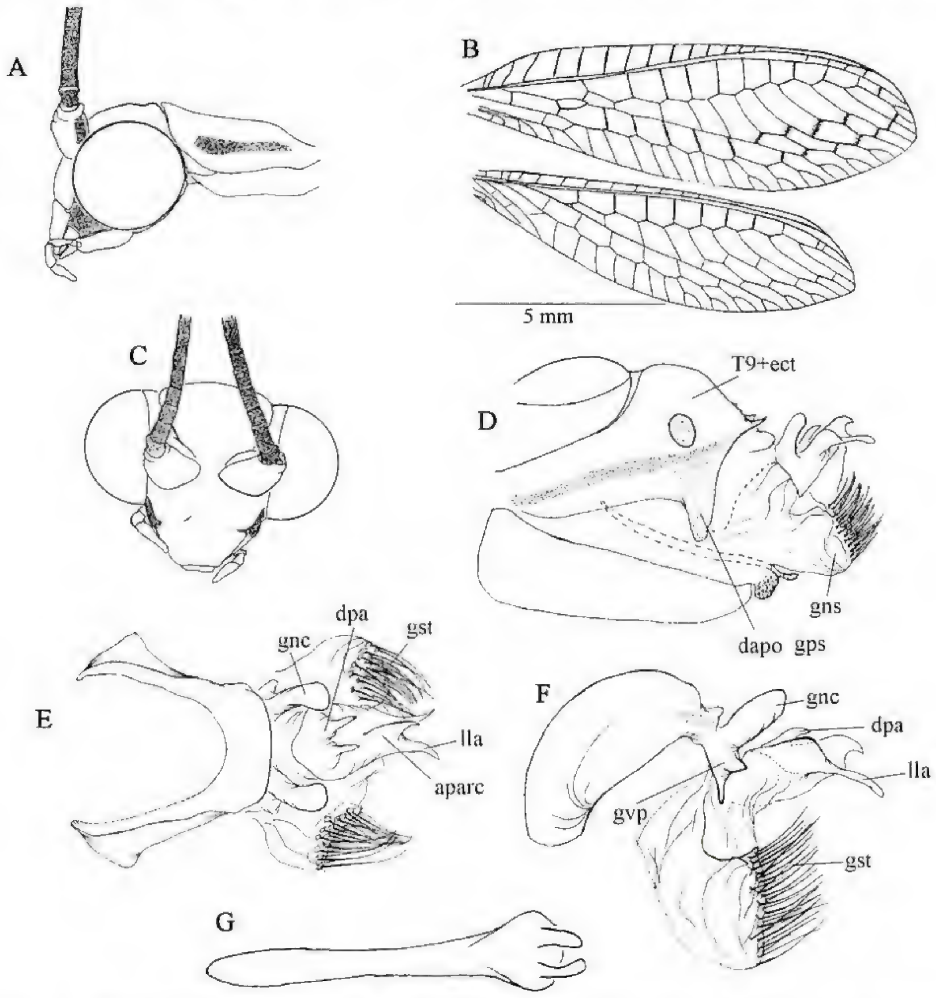


FIGURE 56. *Ceraeochrysa achillea* sp. nov. A. Head and prothorax, lateral view; B. Wings; C. Head, frontal view; D. Male abdomen apex, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Gonapsis.

prolonged ventrally beyond ectoproct. Gonarcal medial arch thick (Fig. 56E); lateral arms elongate, oblong. Each gonocornu a stout rounded process, apically obtuse. Arcessus with basal pair of horns; apical plate with median hook-like process flanked by two long, narrow lobes (Fig. 56F). Gonossacus with two clusters of long setae. Gonapsis elongate with forked apex (Fig. 56G).

HOLOTYPE ♂.— **VENEZUELA: Aragua**, Rancho Grande, 10°20′57″N, 67°35′10″W, 1100 m, 24–31 October 1966, SS & WD Duckworth (USNM).

MATERIAL EXAMINED.— **PANAMA: Panama**, Taboga Island, 8°47′39″N, 79°33′40″W, 18 February 1912, A. Busck. (1♂ – USNM); Tabogilla Island, 20 February 1912, A. Busck (1♀ – USNM); **VENEZUELA: Aragua**, Rancho Grande, 10°20′57″N, 67°35′10″W, 1100 m, 24–31 October 1966, S.S. & W.D. Duckworth (1♂- holotype)(USNM).

GEOGRAPHICAL DISTRIBUTION.— Panama, Venezuela.

ETYMOLOGY – The name comes from the word Achilles, a strong and handsome Trojan warrior, and refers to the male thickened gonarcal median arch and large, strong gonocornua.

SPECIES RELATIONSHIPS.— This species is one of nine species in the *lineaticornis* group that have dark antennae; a dark scape stripe; narrow, dark pronotal stripes; tapered mediuncus and arcessus; apically forked gonapsis; and numerous, long gonosetae on the gonosaccus. Other members of this group include *C. berlandi*, *C. infausta*, *C. lineaticornis*, *C. parvula*, *C. curvabilis*, *C. derospogon*, *C. digitata* and *C. panamensis*. Most species in this group have a male ectoproct that is apically tapered and bears setae with thickened bases. In *C. achillea* the dorsal apodeme extends beyond the callus cerci and apex of the ectoproct to form a small apical hook. Two other species have this extension of the dorsal apodeme: *C. curvabilis* and *C. digitata*, however, in *C. curvabilis* this apical hook has become enlarged and there is no ventral lobe of the ectoproct. The apical extension in *C. digitata* terminates in smaller chalazate setae, but the ventral branch of the dorsal apodeme has become a ventrocaudally projected lobe. The gonocornua of *C. achillea* also are ventrally bilobed, while those of *C. curvabilis* and *C. digitata* are simply lobed.

***Ceraeochrysa angusta* Freitas and Penny, sp. nov.**

DIAGNOSIS.— Head and antennae without dark marks; pronotum with pair of posteriolateral dark spots; heavy dark margins of crossveins; small veinlet at base of dcc, dark and swollen anal crossvein, male gonarcus lateral arms greatly expanded to almost touch along midline.

HEAD.— Vertex, frons, clypeus, gena pale, unmarked. Antennal scape, pedicel and flagellum pale, unmarked..

THORAX.— Pronotum yellow with two lateroposterior dark brown spots (Fig. 57A). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 9 mm. Venation slightly incrassate (swollen) when compared with hindwing veins; costal crossveins black not bordered. Veins R-Rs, outer (5) gradates, Psm-Psc crossveins black with dark margins; inner (4) gradates largely bordered; apical marginal forks black; distal cubital cell black with veinlet; base swollen; apex of 1A inflated, black, and margined (Fig. 57B). Hindwing venation pale.

ABDOMEN.— **Male**: Tergite IX + ectoproct without ventral projection (Fig. 57C); apex of sternite VIII + IX with field of small teeth and small projection with teeth. Gonarcal median arch small, narrow; gonarcus lateral arms projected dorsally as "wings" (Fig. 57E, F). Entoprocesses absent. Two dorsally pointed projections at base of arcessus (gonocornua ?); arcessus large, conical, and elongate, with an acutely pointed apex (Fig. 57G). Gonapsis elongate, tubular, with trident-shaped apex (Fig. 57D).

HOLOTYPE ♂.— **PANAMA: Panama**, Cerro Campana, Chica Nature Reserve, 8°39′40″N, 79°56′21″W, 2–5 April1965, SS & WD Duckworth (USNM).

MATERIAL EXAMINED.— See type.

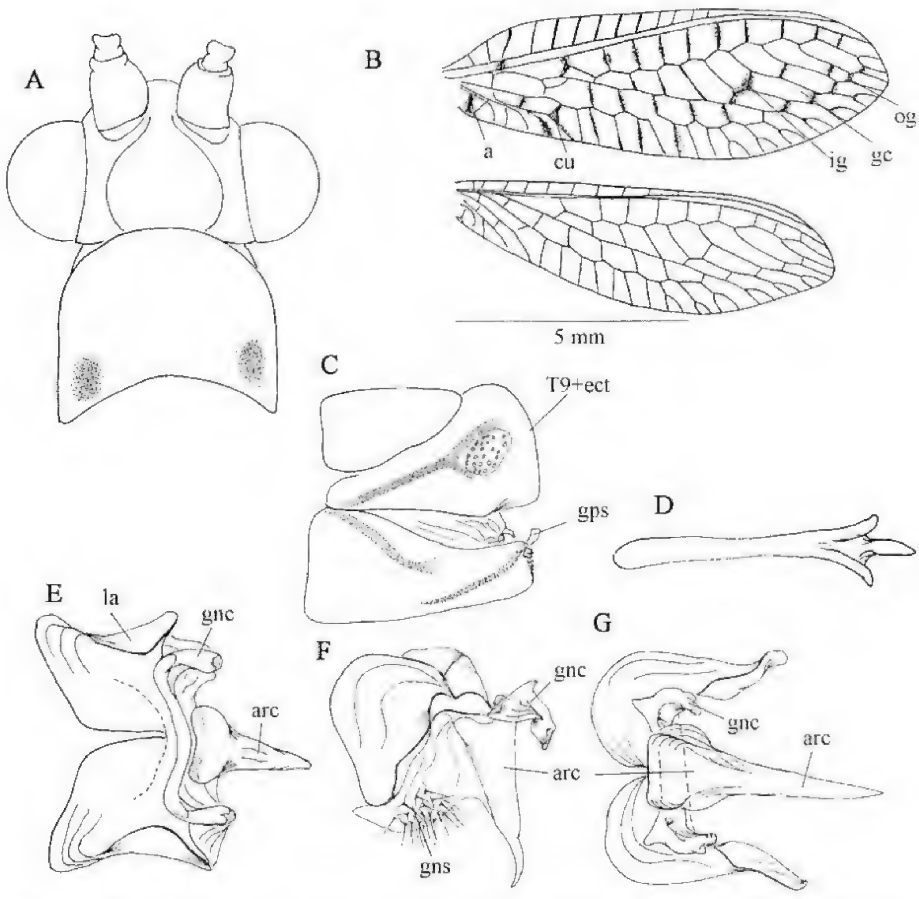


FIGURE 57. *Ceraeochrysa angusta* sp. nov. A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Gonapsis; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Male genitalia, frontal view.

GEOGRAPHICAL DISTRIBUTION.— Panama.

ETYMOLOGY.— The name *angusta* comes from the Latin *angustus*, which means narrow, and refers to the very narrow bridge between the lateral arms of the gonarcus in this species.

SPECIES RELATIONSHIPS.— This species belongs to the *angulata* species group with lateral spots on the pronotum; expanded basal area of fore wing; heavy, dark margins on membrane adjacent to crossveins; distal cubital cell with basal veinlet and dark vein margins; incrassate and darkly bordered anal crossvein. Within this group, *C. angusta* is most closely related to *C. tauberae*, but differs in that *C. angusta* has more expanded lateral arms of the gonarcus, and two well developed lobes at the base of the elongate arcessus.

***Ceraeochrysa belizensis* Freitas and Penny, sp. nov.**

DIAGNOSIS.— This species has as distinctive features: only the basal 8 flagellomeres black, scape and pedicel with wide dorso-lateral stripe, antennal fossa covered by bright red spot.

HEAD.— Pale yellow. Frons, clypeus, gena and maxillary palpi pale, without dark marks. Vertex pale, unmarked except for bright red membranous antennal fossa. Antennal scape and pedicel with quite broad, dark red dorso-lateral stripe, flagellum with first eight flagellomeres black, apically gradually paler (Fig. 58A).

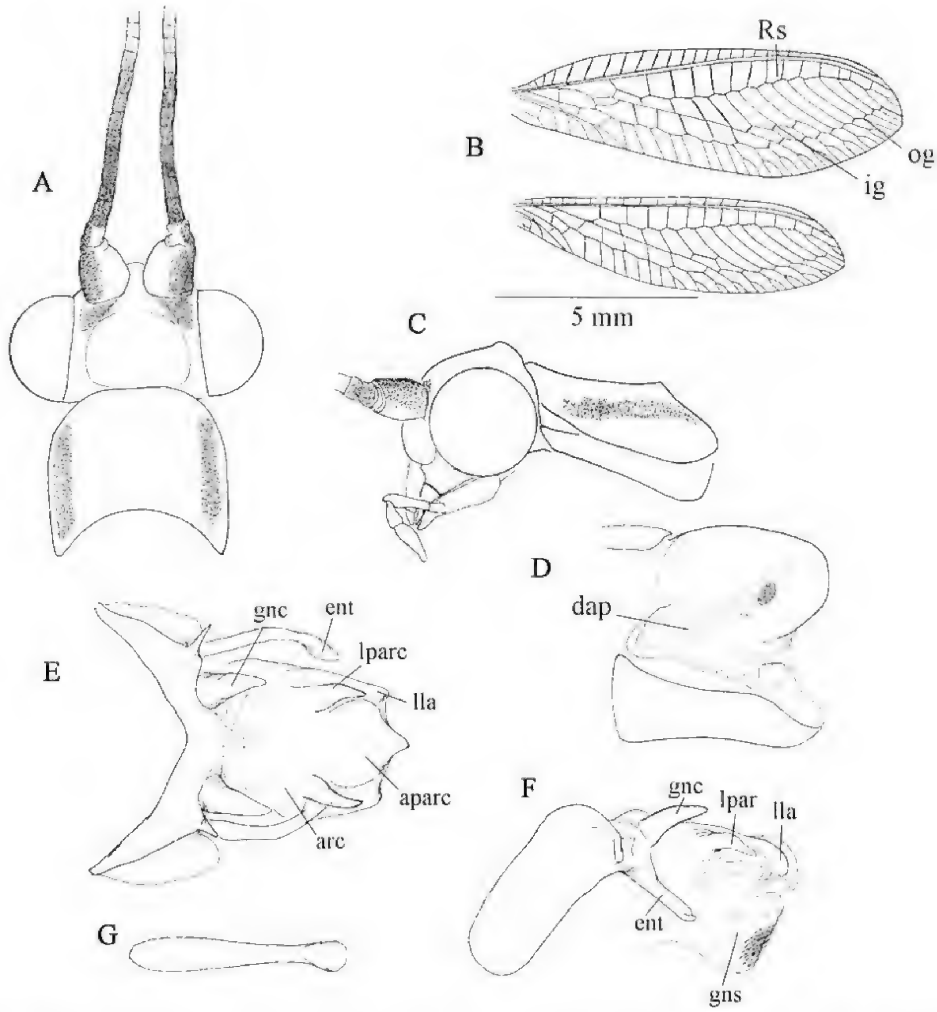


FIGURE 58. *Ceraeochrysa belizensis* sp. nov. A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, lateral view; D. Male genitalia, dorsal view; E. Male abdomen apex, lateral view; F. Male genitalia, lateral view; G. Gonapsis.

THORAX.— Pronotum with lateral, dark red stripe (Fig. 58A, C). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 14 mm. Costal crossveins, basal R-Rs crossveins; Rs-Psm crossveins, inner (3) and outer (9) gradates dark (Fig. 58B). Hindwing venation pale.

ABDOMEN.— Pale green, unmarked. **Male**: Dorsal apodeme of tergite IX + ectoproct enlarged at the fork anterior to callus cerci; ventral branch continued straight caudally (Fig. 58D). Gonarcus medial arch broadly curved; lateral arms narrow with small, ventrally-directed pointed process at juncture with medial arch; gonocornua stout, short, dorsally-directed; entoprocessus long and thin (Fig. 58E, F). Arcessus with pair of dorsal, horn-like processes closely appressed to apical plate; apical plate with small, median hook flanked by pair of rounded lobes. Gonosaccus with medial field of gonosetae. Gonapsis elongate, without lobes (Fig. 58G).

HOLOTYPE ♂.— **BELIZE: Stann Creek**, Sittee Point, 16°48′00″N, 88°15′00″W, 22–30 April 1987. P. Spangler & Faitoute (USNM).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Belize.

ETYMOLOGY.— The name *belizensis* refers to the country of Belize where this species was first recognized.

SPECIES RELATIONSHIPS.— The most distinctive characteristic of this species is the reddish coloration on the dorsal side of the antennal fossa. It shares this characteristic with *C. smithi*, along with the dark basal flagellomeres. However, *C. belizensis* has pale medial scape, whereas *C. smithi* has an entirely dark red scape. The male genitalia of the two species are entirely different. While the male of *C. belizensis* has an undifferentiated sternite VIII + IX and gonapsis, those of *C. smithi* are highly modified. The gonocornua of *C. belizensis* are wider apart and more divergent than in *C. smithi*. The gonareal complex is also quite different, with much longer entoprocesses in *C. belizensis*.

***Ceraeochrysa bitacornua* Freitas and Penny, sp. nov.**

DIAGNOSIS.— This species has black antennal flagellum, vertex yellow golden, lateral red stripes on pronotum and bordered gradates. The very short gonocornua and long narrow arcessus are distinctive.

HEAD.— Vertex frons, clypeus, gena, maxillary palpi, and vertex pale, without dark markings. Antennal scape and pedicel reddish-brown; flagellum black (Fig. 59A).

THORAX.— Pronotum pale with brown lateral stripe (Fig. 59B). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 10 mm; middle costal crossveins dark; R-Rs crossveins dark, inner(4) and outer (6) gradates parallel, black and dark bordered; other veins pale (Fig. 59B). Hindwing venation pale.

ABDOMEN.— Pale green, unmarked. **Male**: Apex of tergite IX + ectoproct deeply cleft in dorsal view. Dorsal apodeme forked at callus cerci, not prolonged caudally (Fig. 59C). Gonarcus medial arch v-shaped with large, ovate lateral arms; gonocornua tiny, with pair of lateral curved processes. Arcessus large, elongate, tapered to single terminal point (Fig. 59D, E). Gonosaccus with dense field of long gonosetae. Membranous genital atrium terminates caudally in two dentate knobs (Fig. 59F). Gonapsis elongate with trifurcate apex, the medial lobe longer than the lateral lobes (Fig. 59G).

HOLOTYPE ♂.— **VENEZUELA: Aragua:** Rancho Grande, 10°20′58″N, 67°41′08″W, 11–15 January 1966, S.S. & W.D. Duckworth (USNM).

MATERIAL EXAMINED.— see type.

GEOGRAPHICAL DISTRIBUTION.— Venezuela.

ETYMOLOGY.— The word *bita* comes from the Anglo-Saxon for little, or bit, and refers to the tiny gonocornua of this species.

SPECIES RELATIONSHIPS.— This species appears to be most closely related to the poorly known *C. fiebrigi* from Paraguay. They both have a rufous antennal scape and dark basal flagellomeres. Because *C. fiebrigi* is known only from the female, the wing venation formed the basis for our taxonomic decision to recognize this species. The fore wing venation of *C. bitacornua* has much more dark shading of the gradate crossveins and the cells formed by the two gradate series are much further apart, to form much more elongate cells.

REMARKS.— See *C. fiebrigi*.

***Ceraeochrysa chiricahuae* Freitas and Penny, sp. nov.**

DIAGNOSIS.— This species has a considerable number of red markings. There are red marks on

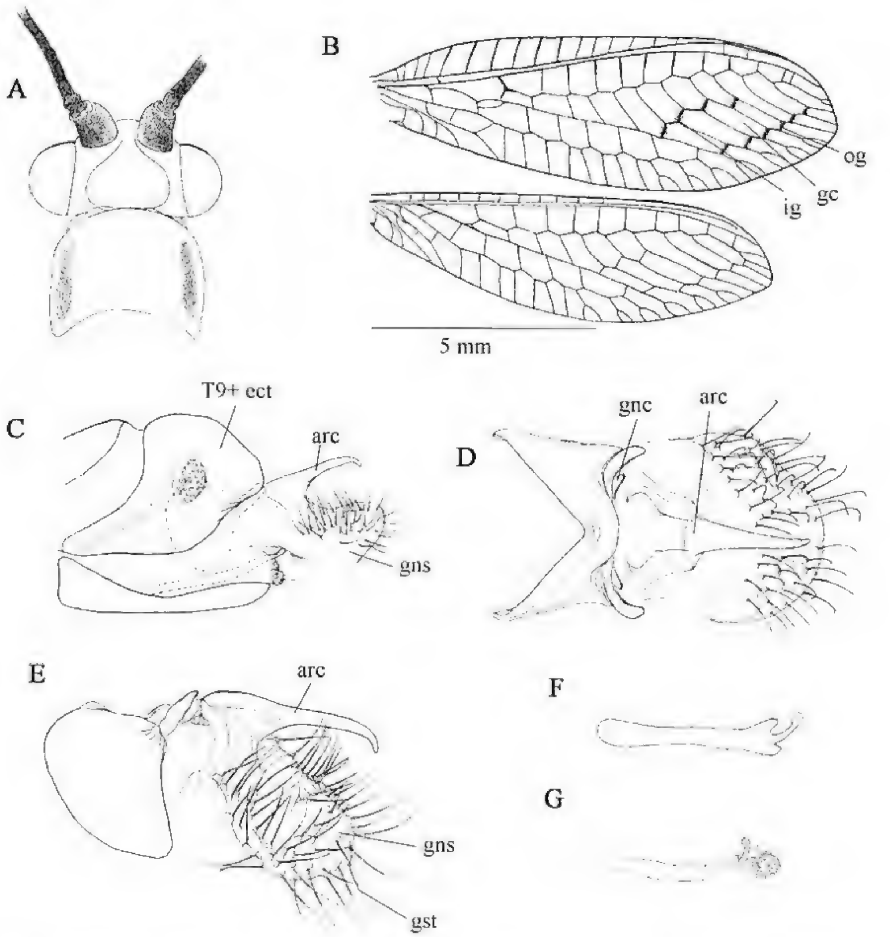


FIGURE 59. *Ceraeochrysa bitacornua* sp. nov. A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Male genitalia, dorsal view; E. Male genitalia, lateral view; F. Gonapsis, dorsal view; G. Gonapsis, lateral view.

frons, vertex, pronotum, mesonotum, and abdominal tergites. Tergite IX + ectoproct does not have a ventral projection. The arcessus is a narrow plate with a tiny apical tooth.

HEAD.— Vertex pale yellow with red marks on vertex and near ocular margins (post-ocular red markings), raised medial area with suffused red marks (Fig. 60A). Frons with bright red transverse band below antennal fossa (Fig. 60C). Gena with thin red stripe (Fig. 60E). Maxillary and labial palpi dorsally black. Antennal scape, pedicel, and flagellum pale, unmarked.

THORAX.— Greenish, yellow to white medially. Pronotum with pair of anterior red spots and submedial red stripes (Fig. 60A). Meso- and metanota with red spots. **Wings**: Fore wing length 14 mm; costal crossveins with black apices; inner (6) and outer (6) gradates black; Rs veins between inner and outer gradates very sinuous (Fig. 61B). Hindwing gradates black, costal crossveins with black apices.

ABDOMEN.— Pale, with pair of red spots on each tergite (Fig. 60D,G). **Male**: Gonarcus medial arch only slightly curved; lateral arms large, oval, vertical; gonocornua short, tapered, acutely pointed apically, bases medially appressed (Fig. 60F). Arcessus inside of eversible gonosaccus; apical plate narrow, ventrally deflexed, with tiny apical tooth (Fig. 60I). Gonapsis long with anterior

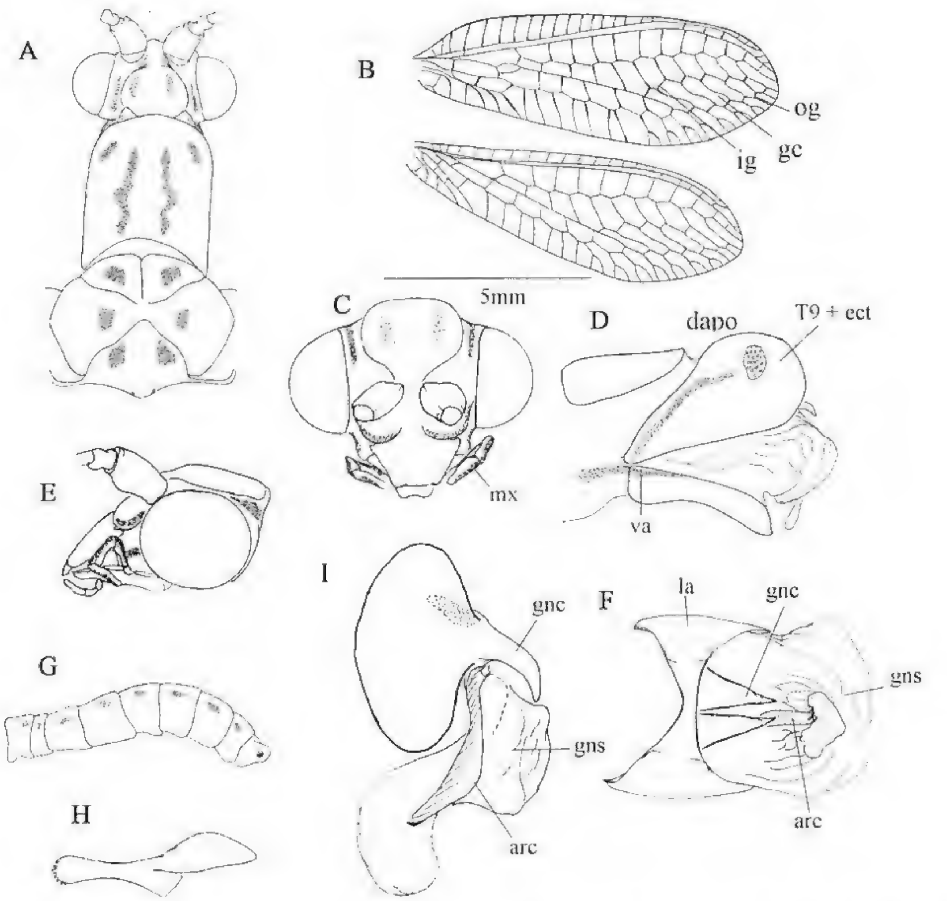


FIGURE 60. *Ceraeochrysa chiricahuae* sp. nov. A. Head, pro- and mesothorax, dorsal view; B. Wings; C. Head, frontal view; D. Male abdomen apex, lateral view; E. Head, lateral view; F. Abdomen, lateral view; G. Male genitalia, lateral view; H. Male genitalia, dorsal view; I. Gonapsis.

dentate apex and posterior extremity curled (Fig. 60H). Dense long setae on abdominal apex.

MATURE LARVA. (as *C. placita*). – Intermandibular mark absent; epicranial mark narrow, not extended laterally to edge of cervical margin; head with submedian mark elongate, extended from antenna posteriorly to cervical margin; epicranial mark extended from external margin of mandibles posteriorly to cervical margin; mesothoracic spiracles borne on prominent tubercles (Tauber and de Leon 2001).

HOLOTYPE ♂.— **USA: Arizona,** Cochise Co., Rustler Park, 31°54′40″N, 109°16′50″W, 6 August 1991, R. & J. Robertson (CAS).

MATERIAL EXAMINED.— **USA: Arizona**, Cochise Co, Chiricahua Mountains, East Turkey Creek, 10 July 1966, R.G. Beard (1♂ – TAMU); Onion Saddle, 7600 ft. [2316 m], 7 July 1966, R.E. Dietz (1♂, 1♀ – TAMU); 24 July 1966, R.E. Dietz (1♂, 1♀ – TAMU); 4 Aug. 1966, R.E. Dietz (1♀ – TAMU); Pinery Canyon, 11 Aug. 1966, R.E. Dietz (1♀ – TAMU); Rustler Park, 9 August 1991, R. &J. Robertson (9♂♂-holotype and 8 paratypes)(CAS); Rucker Canyon, 4 August 1991, R. & J. Robertson (3♂♂,4♀♀-CAS); **California:** Lake Co., Clear Lake, 13 July 1918, C.L. Hubbs (1? – FMNH); Riverside Co., San Jacinto Mtns., Santa Rosa Peak, 1 August 1995, R. Robertson (1♂-CAS); Tulare Co., Mineral King, August 1979, P. Duelli (1♂2♀♀-CAS); Johnsondale, S. of Sequoia National Park, 25 July 1979 (1♂1♂ CAS); Tulolumne Co., Twain

Harte, 1 Sept. 1963, M. Lundgren (1♀ – TAMU); **Colorado:** Alamosa Co., 5 km wsw California Peak, 2530 m, 3 Aug. 2001, J.D. Oswald (1♂ – TAMU); **New York:** Albany Co., Rensseloerville, E.N. Huyck Prerserve, 1600 ft. [488 m], E.G. MacLeod, 19 Aug. 1961 (4♀♀ – TAMU); 2 Sept. 1964 (1♀ – TAMU); 12 Aug. 1966 (1♂ – TAMU); 17 Aug. 1966 (6♂♂ – TAMU); 18 Aug. 1966 (1♂ – TAMU); **North Carolina:** Yancey Co., Blue Ridge Parkway, Crabtree Meadows, 21 June 1962, G.L. Bush (1♂ – TAMU); **West Virginia:** Hardy Co., 3 mi ne Mathias, 1–24 Aug. 2000, D. Smith (1♀ – TAMU); 10–30 Aug. 2001, D. Smith (1♀ – TAMU); 22 Sept. to 12 Oct. 2001, D. Smith (1♀ – TAMU).

GEOGRAPHICAL DISTRIBUTION.— USA.

BIOLOGY.— Eggs are laid singly on short stalks on the bark of medium-sized to large deciduous and evergreen trees from mid-July to mid-September. Eggs have a relatively long incubation periods, taking 12 to 16 days to hatch. Young larvae place small pieces of bark fragments and exuviae on their backs. After the first molt, the 2nd instar larva enters developmental diapause and remains dormant throughout the winter months. From mid-April to mid-May the larva again becomes active and molts to 3rd instar, then moves to the foliage and begins to actively feed. Cocoons are spun from mid-May to mid-June and emergence begins in mid-June (Tauber et al. 1998).

ETYMOLOGY.— The name is derived from the Chiricahua band of Apache native Americans whose traditional home is in the Chiricahua Mountains of southeastern Arizona where many specimens of this species have been collected.

SPECIES RELATIONSHIPS – For many years a species has been identified as *C. placita* that has bright red markings on the head, thorax, and abdomen. However, the syntype series from Colorado is much darker in coloration. To complicate matters even more, the reddish specimens from the northeastern U.S.A. and Canada have somewhat different markings than the populations in the western U.S.A. The reddish line that runs along the top of the gena and above the clypeus, as well as the red line laterally on the vertex tend to be absent, or possibly fade easily in the eastern population. The thorax has a dorsomedial line that is quite pale, almost white. It is bordered laterally by some reddish coloration that is darkest at mid-length and fades out both anteriorly and posteriorly, to give this border the aspect of a faint pink spot in northeastern specimens. The dark form of *C. placita*, as exemplified by the syntypes, and the reddish form are clearly closely related. The male genitalia both have a gonarcus with lateral arms that are quite long vertically and gonocornua that are close together and triangular in shape. However, the gonocornua of the dark form are much longer than all populations of the reddish form. They extend well beyond the lateral arms of the gonarcus. So, we have decided that the reddish form belongs to a separate species, *C. chiricahuae*.

REMARKS.— Tauber (2003) proposed placing this species (as *C. placita*) in *Chrysopodes* based on characteristics of the larva. In doing so, she ignored the elongate, tubular nature of the male gonapsis, probably the most distinctive feature used to define *Ceraeochrysa*. The two genera are clearly closely related, and there are a couple of species of *Chrysopodes* that have a gonapsis, but that structure is short, flat, and broad when it exists in *Chrysopodes*. The dual development of an elongate, tubular gonapsis in *Chrysopodes* and *Ceraeochrysa* seems highly unlikely, as does development of secondary short, broad gonapsis from an elongate, tubular one and then complete loss of this structure in the evolution of *Chrysopodes*. The placement of *C. chiricahuae* in *Chrysopodes* also creates a situation as to how to define the genus *Ceraeochrysa*. And, it raises the issue of the need to have an identified larval form in order to place a species in the proper genus. Because larvae of the vast majority of species in both genera are completely unknown, this placement raises doubts about dozens of other species and great nomenclatorial instability.

This species has the typical male sclerotized structures of *Ceraeochrysa*. That is, the arcessus is an elongate, membranous tube with an apical sclerotized plate with small tooth at the end. *Chrysopodes* has a short, broad, triangular arcessus. The drawings in Tauber (2003) are greatly sim-

plified and lacking the detail necessary to differentiate between them. For the above reasons, we reject Tauber's hypothesis and have returned this species to *Ceraeochrysa*.

***Ceraeochrysa curvabilis* Freitas and Penny, sp. nov.**

DIAGNOSIS.— This species has black antennae (at least 11 basal flagellomeres), scape and pedicel laterally black striped; gena black; fore wing with transverse veins darkly margined; dorsal apodeme of ectoproct with curved acute process caudally.

HEAD.— Vertex, frons, clypeus, and maxillary and labial palpi pale, unmarked. Gena black dorsally; pale ventrally (Fig. 61C, E). Antennal scape and pedicel black laterally (Fig. 61A); flagellum basal 11 flagellomeres black, gradually paler apically.

THORAX.— Pronotum pale with red lateral stripe. Meso- and metanota pale, unmarked. **Wings**: Fore wing length 13 mm. Longitudinal veins pale; transverse veins black; R-Rs crossveins, inner

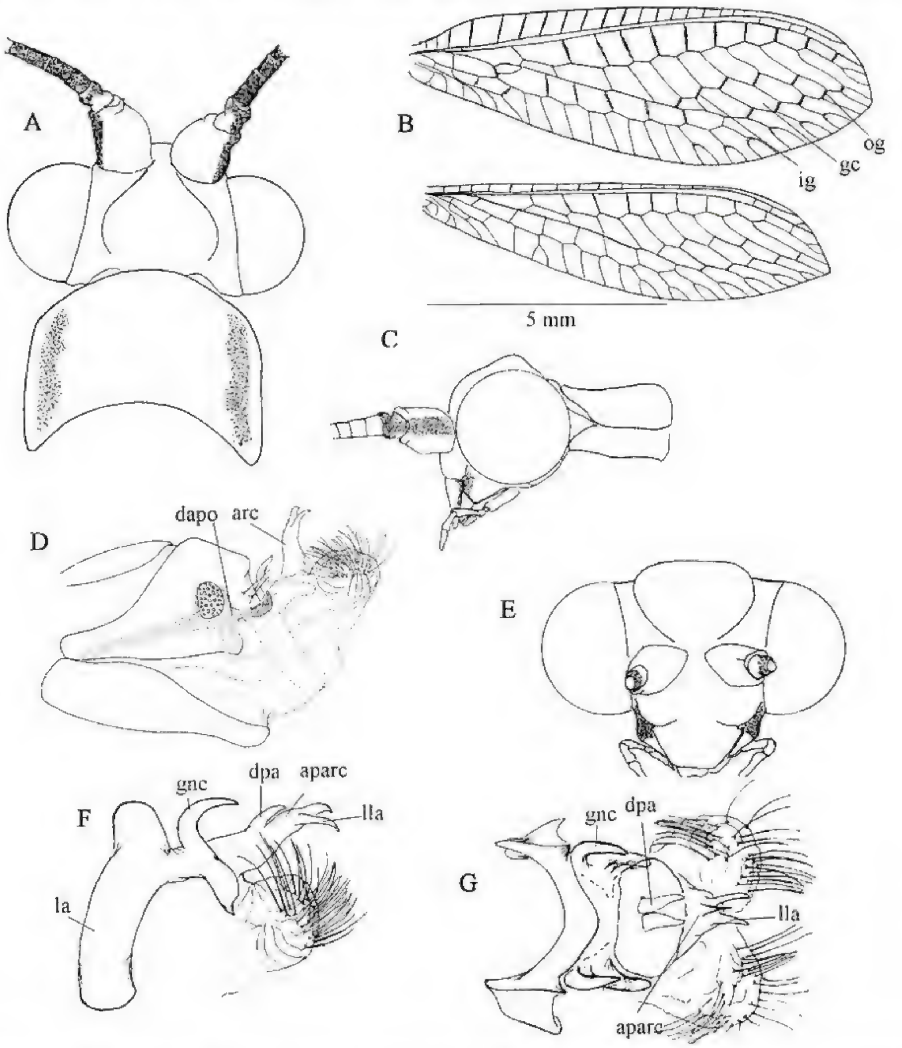


FIGURE 61. *Ceraeochrysa curvabilis* sp. nov. A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, Lateral view; D. Male abdomen apex, lateral view; E. Head, frontal view; F. Male genitalia, lateral view; G. Male genitalia, dorsal view.

(5) and outer (5) gradates (Fig. 61B), Psm-Psc transverse veins, marginal forks and apices darkly bordered, hindwing venation pale.

ABDOMEN.— Pale green, unmarked. **Male**: Tergite IX + ectoproct with large chalazate setae on posterior margin. Dorsal apodeme caudally extended beyond posterior margin of ectoproct to form a medially curved process. Ventral branch of dorsal apodeme extends to ventral margin of ectoproct (Fig. 61D). Gonarcus medial arch broadly curved, lateral arms narrow. Gonocornua widely separated, strongly curved dorsally (Fig. 61F, G). Arcessus triangular, with two dorsal projections; apex tri-lobled, with long, acutely-pointed lateral lobes. Gonosaccus bi-lobed, each lobe with clusters of quite long setae. Gonapsis elongate, tubular.

HOLOTYPE ♂.— **COSTA RICA: Puntarenas,** S. Rincon de Osa, 8°42′00″N, 83°29′00″W, 4–12 March 1969, J.K. Sheldon (INBio).

MATERIAL EXAMINED.— Type.

GEOGRAPHICAL DISTRIBUTION.— Costa Rica

ETYMOLOGY.— *Curvabilis* comes from the Latin *curvus*, which means bent, and refers to the unusual hook-like processes at the end of the male ectoprocts.

SPECIES RELATIONSHIPS.— *Ceraeochrysa curvabilis* is part of the *lineaticornis* species group characterized by dark antennal flagellum, dark scape stripe, dark gena, narrow, dark stripes on pronotum, darkly margined crossveins in the fore wing and males with bilobed gonosaccus and elongate arcessus with long, acute lateral lobes apically. Two species in this group have the dorsal apodeme extended caudally as an apical hook: *C. achillea* and *C. curvabilis*. Males of *Ceraeochrysa achillea* have a small projection at the apex of the ectoprocts, but in this species it is much smaller and not so heavily sclerotized. The ventral branch of the dorsal apodeme is also much longer in *C. achillea*.

***Ceraeochrysa derospogon* Freitas and Penny, sp. nov.**

DIAGNOSIS.— This species has an antennal scape and pedicel with a black stripe laterally and black flagellum. The gena is black anteriorly and pale posteriorly. The clypeus has a black stripe laterally. Males have a ventral extension of the ectoproct, elongate, triangular arcessus with single apical point, and bilobed gonosaccus with long setae.

HEAD.— Pale yellow. Vertex pale, unmarked. Frons pale, unmarked. Clypeus with thin black stripe laterally. Gena black anteriorly, near frons and pale posteriorly (Fig. 62C, D). Antennal scape with lateral black stripe; pedicel black (Fig. 62A); antennal fossa near base of scape marked with red.

THORAX.— Pronotum pale with lateral dark red stripe (Fig. 62A). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 11 mm. Venation pale with broad black marks, mainly along transverse veins; costal crossveins black; radial sector very dark in middle; R-Rs transverse veins dark posteriorly; Psm crossveins anterior apices black; inner (4) and outer (6) gradates parallel, black; marginal forks black (Fig. 62B). Hindwing venation pale.

ABDOMEN.— Abdomen pale green, without dark markings. **Male**: Tergite IX + ectoproct with ventral branch of dorsal apodeme projected ventrocaudally beyond margin of ectoproct (Fig. 62E). Gonarcus medial arch stout and short; lateral arms broadly triangular. Gonocornua small, medial, dorsally-directed, with bases juxtaposed. Entoprocesses long and thin. Arcessus with basal pair of dorsal processes; apical plate with thin, medial hook and lateral lobes (Fig. 62F, H). Gonosaccus with field of long setae. Gonapsis elongate, forked at posterior apex (Fig. 62G).

HOLOTYPE ♂.— **MEXICO: Chiapas:** Teopisca, 16°31′58″N, 92°28′10″W, 9 July 1966, O.S. Flint, Jr. & Ortiz (USNM).

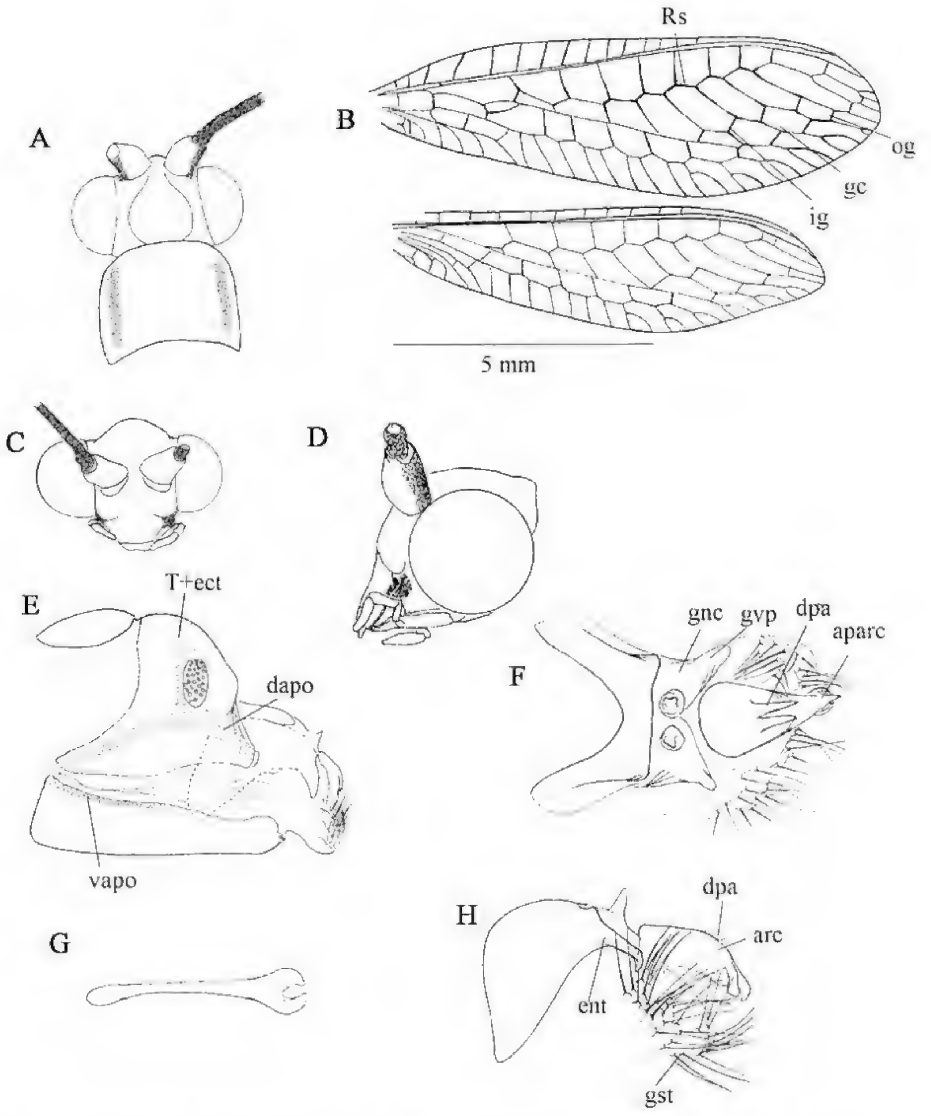


FIGURE 62. *Ceraeochrysa derospogon* sp. nov. A. Head and prothorax, dorsal view; B. Wings; C. Head, frontal view; D. Head, lateral view; E. Male abdomen apex, lateral view; F. Male genitalia, dorsal view; G. Gonapsis; H. Male genitalia, lateral view.

MATERIAL EXAMINED.— **MEXICO: Chiapas:** Teopisca, 16°31′58″N, 92°28′10″W, 9 July 1966, O.S. Flint, Jr. & Ortiz (1♂ – holotype)(USNM); **GUATEMALA**: **El Progreso**, Finca La Cajeta, 12–20 August 1965, O.S. Flint, Jr. & Ortiz (USNM).

GEOGRAPHICAL DISTRIBUTION.— Mexico, Guatemala

ETYMOLOGY.— The name *derospogon* comes from the Greek words *deros*, meaning long, and *pogon*, which means beard, and refers to the numerous, long setae of the male gonosaccus.

SPECIES RELATIONSHIPS.— This species is part of the *achillea* species group that have dark antennal flagellum, dark genal spot, dark markings along the fore wing crossveins, male with extensions of the dorsal apodeme, a pair of small lobes at the base of the arcessus, and long setae

on the gonosaccus. *Ceraeochrysa derospogon* has a ventral extension of the male ectoproct formed by the ventral branch of the dorsal apodeme, similar to *C. achillea* and *C. curvabilis*, but lacks the apical hooks of the other two species.

***Ceraeochrysa digitata* Freitas and Penny, sp. nov.**

DIAGNOSIS.— The antennal flagellum black, lateral dark red stripe on scape, dark stripe on gena and bordered veins on fore wing indicate that this is a member of the *achillea* species group. The extremely long, apically forked entoprocesses and blunt-tipped gonocornua separate this from other members of the group.

HEAD.— Vertex yellow with pair of red spots at base of antennal fossa and pair of post-ocular red spots. Frons and maxillary palpi pale. Clypeus pale with dark lateral stripe. Gena black dorsally, pale ventrally (Fig. 63C, D). Antennal scape with dark reddish brown lateral stripe (Fig. 63A); pedicel black-ringed; basal 11 flagellomeres black, gradually paler apically.

THORAX.— Pronotum green with red lateral stripe (Fig. 63A). Mesonotum pale with red spot at lateral angle of prescutum. **Wings**: Fore wing length 11 mm. Longitudinal veins pale; transverse veins black with paler border (Fig. 63B). Inner (4) and outer (5) gradates parallel, dark. Hindwing length 9 mm; venation pale.

ABDOMEN.— Green without dark marks. **Male**: Apex of ectoproct with setae with large, conical bases. Dorsal apodeme forked anterior to callus cerci; ventral fork broad, projects ventrocaudally beyond margin of ectoproct (Fig. 63E). Gonarcus medial arch with curved, ovate lateral arms; gonarcal lateral arms with long posterior projections that terminate in apical fork (Fig. 63F). Gonocornua dorsally projected with rounded apex. Arcessus with pair of basal horns (Fig. 63H); apical plate trilobed, the median lobe hook-like. Gonosaccus with two clusters of long setae lateral to a field of microteeth. Gonapsis with forked apex (Fig. 63G).

HOLOTYPE ♂.— **COSTA RICA: Puntarenas,** Rincon de Osa, 8°42′00″N, 83°29′00″W, 4–12 March1969. J.K. Sheldon (INBio).

MATERIAL EXAMINED.— See type.

GEOGRAPHICAL DISTRIBUTION.— Costa Rica.

ETYMOLOGY.— *Digitatus* comes from the Latin word *digitus*, meaning finger-like, and refers to the elongate, rounded form of the male gonocornua.

SPECIES RELATIONSHIPS.— This species is a part of the *lineaticornis* species group with dark antennae, dark gena, dark shading of the fore wing crossveins, and males with elongate tapered arcessus with basal pair of small, pointed lobes. *Ceraeochrysa digitata* does not have the dorsal apodeme extended caudally as a projection and can be separated from all other members of the group by the broad ventral branch of the dorsal apodeme; widely-spaced, apically rounded gonocornua, and small medial teeth on the gonosaccus. The female is still unknown.

***Ceraeochrysa divaricata* Freitas and Penny, sp. nov.**

DIAGNOSIS.— Species with black antennae; broad, dark brown lateral scape stripe; some transverse veins on fore wing with dark margins. Male genitalia with elongate ventral apodeme, divergent gonocornusa, and large divergent pair of lobes at base of arcessus.

HEAD.— Vertex, frons, clypeus, maxillary palpi, and gena pale, unmarked. Antennal scape and pedicel with broad, dorsolateral, dark brown stripe (Fig. 64A, C); basal seven flagellomeres black, remainder of flagellum fuscous.

THORAX.— Pronotum pale with dark red lateral stripes (Fig. 64A). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 11 mm. Basal costal crossveins black; R-Rs crossveins black,

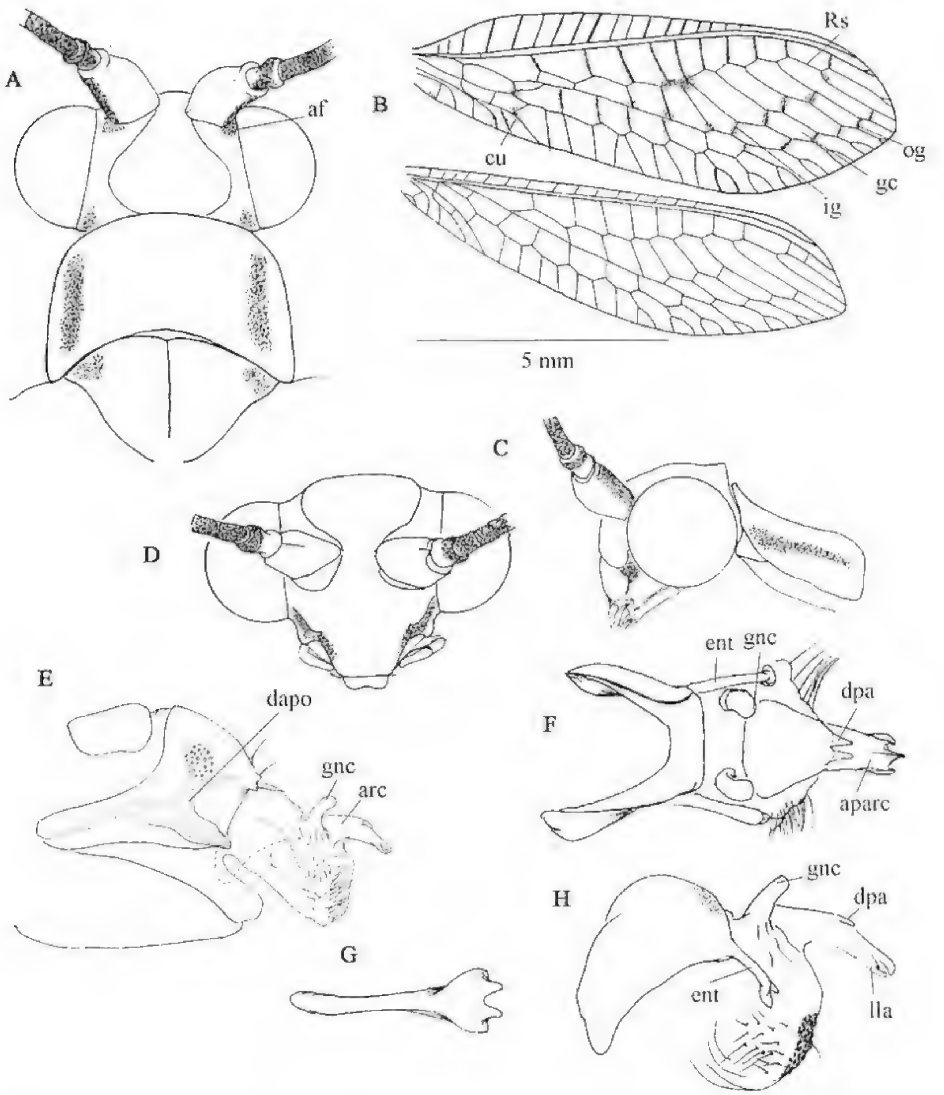


FIGURE 63. *Ceraeochrysa digitata* sp. nov. A. Head and prothorax, dorsal view; B. Wings; C. Head and prothorax, lateral view; D. Head, frontal view; E. Male abdomen apex, lateral view; F. Male genitalia, dorsal view; G. Gonapsis; H. male genitalia, lateral view.

basal Rs-Psm crossveins black; inner (3) and outer (7) gradates parallel, black (Fig. 64B). Hindwing venation pale.

ABDOMEN.— Pale green, unmarked. **Male**: Dorsal apodeme of tergite IX + ectoproct without ventral projection. Ventral apodeme prominent, elongate, extended to apex of sternite VIII + IX in membrane above sternite (Fig. 64D). Gonarcal arch quite narrow, with large, quadrate lateral arms. Gonocornua pointed, divergent. Entoprocesses well developed as elongate, blunt-tipped lobes (Fig. 64E,F). Arcessus broad with pair of large, basal, dorsal processes; apex of median plate with stout medial hook and lateral minor lobes. Gonapsis elongate, undifferentiated rod (Fig. 64G).

HOLOTYPE ♂.— **COSTA RICA: Guanacaste**, Finca La Pacifica, 3 February 1969, J.K. Sheldon (INBio).

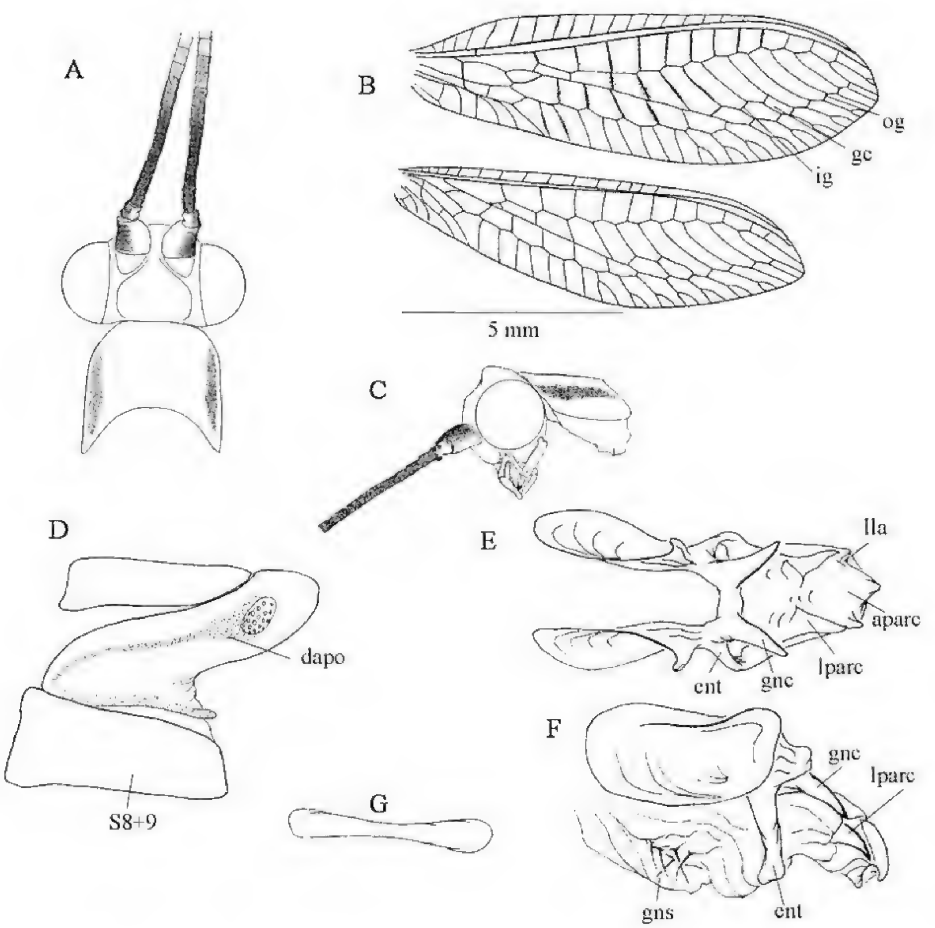


FIGURE 64. *Ceraeochrysa divaricata* sp. nov. A. Head and prothorax, dorsal view; B. wings; C. Head and prothorax, lateral view; D. Male abdomen apex, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Gonapsis.

MATERIAL EXAMINED.— **COSTA RICA: Guanacaste**, Finca La Pacifica, 10°27′47″N, 85°06′30″W, 3 February 1969, J.K. Sheldon (2♂♂ – holotype and paratype)(INBio and CAS).

GEOGRAPHICAL DISTRIBUTION.— Costa Rica.

ETYMOLOGY.— The name of this species comes from the Latin *divaricatus*, which means to spread apart, and refers to the divergent gonocornua of the male.

SPECIES RELATIONSHIPS.— In the least advanced members of *Ceraeochrysa* males have a dorsal apodeme structurally supporting tergite IX and ectoproct, and ventral apodeme supporting sternite VIII + IX that articulate on one another basally. The dorsal apodeme caudally ends near the callus cerci. This is the state found in *C. divaricata*. In more advanced states, the dorsal apodeme of males is forked just in front of the callus cerci, with the ventral branch extended caudally or ventrally as hooks or projections. This is the state found in the some members of the *lineaticornis* group. In the *C. cincta* group, the ventral branch of the dorsal apodeme has migrated further anteriorly and has become more curved. Although *C. divaricata* is primitive with regards to the male dorsal apodeme, in many other ways it ressembles males of *C. caligata*. Males of both species have a broad arcessus with pair of basal lobes and elongate entoprocesses, as well as gonapsis in the

form of a simple, undifferentiated rod. In addition to the different shape of the male dorsal apodeme, they differ in that *C. divaricata* has antennae with dark flagellomeres basally and a much broader scape stripe, and darkened margins to basal crossveins in the fore wing. Males of *C. divaricata* have larger, more divergent gonocornua than C. *caligata*.

***Ceraeochrysa forcipata* Freitas and Penny, sp. nov.**

DIAGNOSIS.— This species is recognized primarily by structures of the male genitalia: tergite IX + ectoproct is deeply bifurcated to form two elongate dorsal lobes, and sternite VIII + IX has a pair of small lobes covered with gonocristae at the posteriolateral corners; the gonapsis is broadly inflated posteriorly.

HEAD.— Vertex, frons, clypeus and gena yellow, unmarked. Maxillary palpi amber. Antennal scape with brown lateral spot (Fig. 65A); pedicel and flagellum pale.

THORAX.— Pronotum pale with pale red, lateral stripe (Fig. 65A). Meso- and metanota pale, unmarked. **Wings**: Fore wing length 11 mm. Venation pale with costal crossveins dark at the middle; base of Rs and radial crossveins dark; inner gradates (8) black, outer gradates (8) pale, series parallel (Fig. 65B). Hindwing venation pale.

ABDOMEN.— Yellow, unmarked. **Male**: Tergite IX + ectoproct forked into two deeply cleft lobes densely covered by long setae (Fig. 65C, D). Dorsal apodeme branched in front of callus cerci with vertical short, thick, dorsal branch; short, pointed, ventral branch; and thin, posterior branch. Sternite VIII + IX terminates in a two lateral processes covered with gonocristae (Fig. 65E). Gonarcus medial arch broad, plate-like; lateral arms ovate. Gonocornua widely separated, elongate, with horn-like apex. Arcessus large, median plate with long dorsal projection (Fig. 65F, G). Gonosaccus with two clusters of long setae. Gonapsis short, apex enlarged (Fig. 65H). **Female** – spermatheca short with small spermathecal gland (Fig. 65I, J).

HOLOTYPE ♂.— **BOLIVIA: Cochabamba**, Carrasco, Siberia, 1650 m, January 1964, F.M. Walz (CAS).

MATERIAL EXAMINED.— **BOLIVIA: Cochabamba**, Carrasco, Siberia 1650 m, January 1964, F.M. Walz (3♂♂, 15♀♀).

GEOGRAPHICAL DISTRIBUTION.— Bolivia.

ETYMOLOGY.— The species name *forcipata* comes from the Latin word *forceps*, meaning pincers or tongs, and refers to the two deeply cleft lobes of the male ectoprocts of this species.

SPECIES RELATIONSHIPS.— This species appears to be most closely related to *C. cubana* and *C. sanchezi* by virtue of the lateral lobes at the apex of the male sternite VIII + IX and the broad, weakly arched gonarcus of these species. They can be separated by the dorsal hood of the gonarcus and giant abdominal spiracles of male *C. cubana*, the dark antennae of *C. sanchezi*; and most notably, the deeply cleft tergite IX and ectoprocts of *C. forcipata*.

REMARKS.— We could not locate the type locality "Siberia" on any maps or gazetteers. F.M. Walz was a fairly well-known collector and dealer in Argentina, and there is a locality Siberia in Jujuy Province in northwestern Argentina. However, there is a Carrasco District in Cochabamba Province, Bolivia, and it would not be surprising if there is a small village somewhere in that district named Siberia.

***Ceraeochrysa panamensis* Freitas and Penny, sp. nov.**

DIAGNOSIS.— The largely dark bordered veins of the fore wing combined with the dark red latero-dorsal stripe of antennal scape separates this from other species. There also is a small dark mark near the frons on the gena.

HEAD.— Vertex pale yellow, unmarked except for two pair of small red marks: one pair in

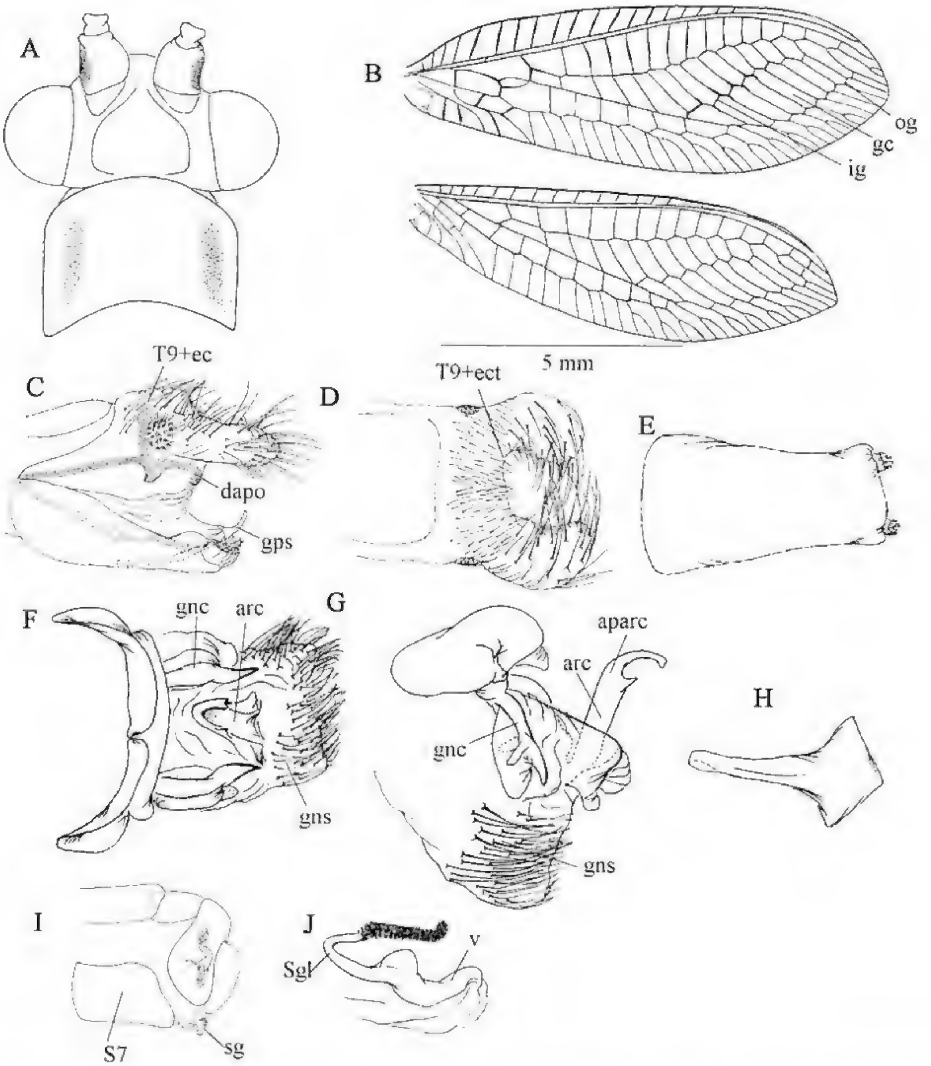


FIGURE 65. *Ceraeochrysa forcipata* sp. nov. A. Head and prothorax, dorsal view; B. Wings; C. Male abdomen apex, lateral view; D. Male abdomen apex, dorsal view; E. VIII + IX sternites, ventral view; F. Male genitalia, dorsal view; G. Male genitalia, lateral view; H. Gonapsis; I. Female abdomen, lateral view; J. Spermatheca.

antennal fossa at base of scape, the other pair at post-ocular margin (Fig. 66C). Frons and clypeus pale, unmarked; gena with small dark mark near frons. Antennal scape pale with lateral red stripe (Fig. 66A); pedicel and flagellum pale.

THORAX.— Pronotum pale, with dark red stripe laterally. Meso- and metanota pale, unmarked. **Wings**: Fore wing length 11 mm. Venation pale with costal crossveins dark, not bordered. R-Rs crossveins, inner (5) and outer (6) gradates, Psm-Psc crossveins dark with broad dark margins; marginal forks black; cubital and anal veins black and darkly margined (Fig. 66B). Inner and outer gradate series parallel. Hindwing pale green, without markings; 4 inner and 5 outer gradates.

ABDOMEN.— Pale, without dark marks. **Male**: Apex of tergite IX + ectoproct and sternite VIII + IX with large tubercles that bear setae. Dorsal apodeme of ectoproct enlarged near callus

cerci and prolonged caudally; apex curved medially into genital atria (Fig. 66D). Gonarcus medial arch thick; lateral arms large, sigmoid-shaped. Gonocornua widely separated, apically incurved and blunt-tipped with ventral projection (entoprocesses apparently absent) (Fig. 66E, F). Mediuncus heavily sclerotized with pair of apical points. Median process of arcessus plate-like with two poorly-defined lateral lobes and medial hook. Gonosaccus with long gonosetae that bear large chalazate bases. Gonapsis elongate, apex with two lateral lobes (Fig. 66G).

HOLOTYPE ♂.— **PANAMA: Panama**, Cerro Campana, Chica, 8°39′40″N, 79°56′21″W, 2–5 April 1965, S.S. & W.D. Duckworth (USNM).

MATERIAL EXAMINED.— see type

GEOGRAPHICAL DISTRIBUTION.— Panama.

ETYMOLOGY.— The name *panamensis* refers to the country of origin of the type specimen.

SPECIES RELATIONSHIPS.— The tapered male ectoproct with chalazate based setae and heavily infuscated fore wings suggests a close relationship with the *lineaticornis* species group. However, unlike other members of this group, *C. panamensis* has pale antennae and the male mediuncus and arcessus are not tapered with elongate lateral lobes at the apex that suggests a somewhat more distant relationship within the group.

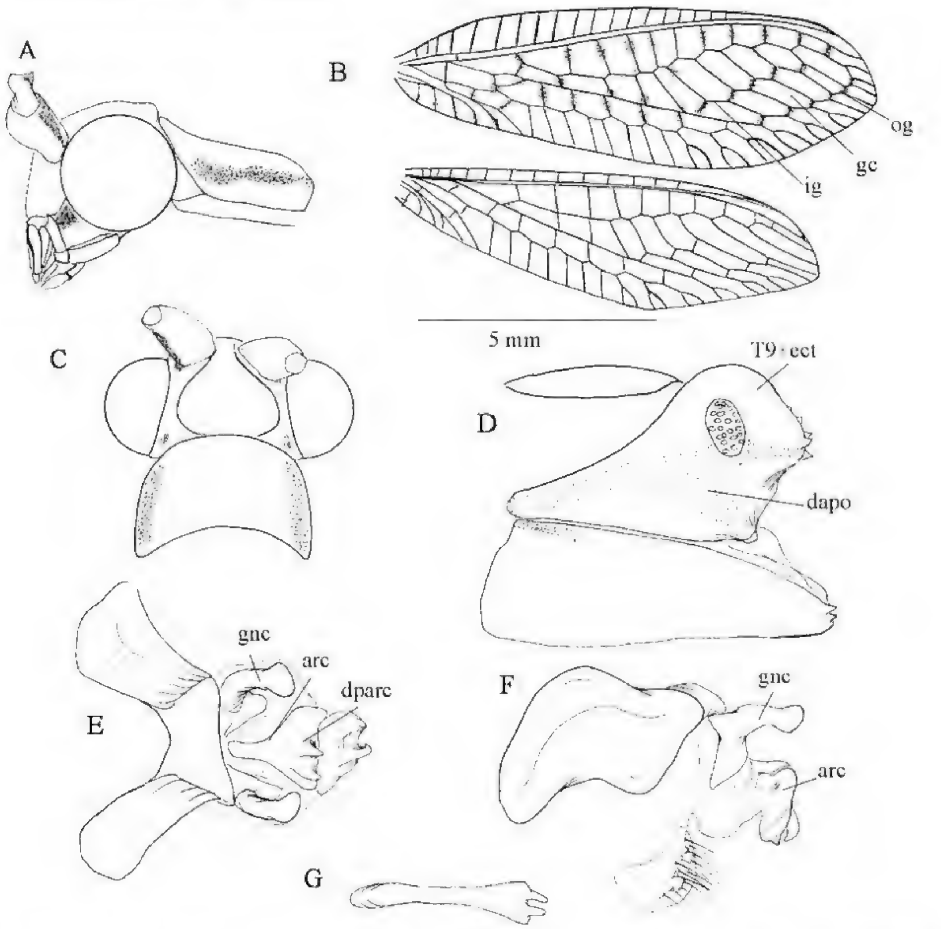


FIGURE 66. *Ceraeochrysa panamensis* sp. nov. A. Head and prothorax, lateral view; B. Wings; C. Head and prothorax, dorsal view. D; Male abdomen apex, lateral view; E. Male genitalia, dorsal view; F. Male genitalia, lateral view; G. Gonapsis.

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A Key to the Brachyuran Megalopae of Native and Invasive Species Inhabiting the San Francisco Bay Estuary

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In light of the recent crab invasions of San Francisco Bay and its estuary, research has increasingly focused on the life history of invasive species such as the Chinese mitten crab, *Eriocheir sinensis* and the green crab, *Carcinus maenas*. It is important that all life history stages of these invasive species are studied. The study of non-native species inhabiting the region is hindered by the lack of a means to identify their post-larval megalopae stage. The motivation of this work was to create a dichotomous key of the brachyuran megalopae of the San Francisco Bay and estuary that includes both native and non-native species. The key was created using species descriptions from published literature; illustrations used in the key were adapted from illustrations in published literature or were drawn from captured specimens. The brachyuran megalopae included in the key are: *Cancer productus*, *Carcinus maenas*, *Eriocheir sinensis*, *Hemigrapsus nudus*, *Hemigrapsus oregonensis*, *Lophopanopeus bellus*, *Lophopanopeus leucomanus*, *Metacarcinus anthonyi*, *Metacarcinus gracilis*, *Metacarcinus magister*, *Pachygrapsus crassipes*, *Pyromaia tuberculata*, *Rhithropanopeus harrisii*, and *Romalaeon antennarius*. Although *Romalaeon jordani* and *Pugettia producta* are also found in the region, these species are not included in the key because their megalopae remain undescribed. Also, little literature is available on the larval descriptions of the pinnotherid crabs present in the San Francisco Bay. Consequently, members of the Pinnotheridae family are grouped together in the key using a specific morphological characteristic described in published literature (Lough 1974).

In order to understand better the life history of the invasive crab species in the San Francisco Bay, it is important to analyze all stages in their life history including the post-larval megalopa stage. Efforts to study these invading organisms have been hampered by our inability to identify the brachyuran megalopae found in San Francisco Bay. To this end, we constructed a dichotomous key to include native brachyuran species and those that had invaded San Francisco Bay as of 2007. Twenty-two brachyuran species have been reported from San Francisco Bay and its estuary (Mooi et al. 2007; Rice and Tsukimura 2007; California Academy of Sciences 2008). *Pugettia producta* and *Romalaeon jordani* have been collected in the Bay and are listed in the Invertebrate Collection catalog of the California Academy of Sciences (California Academy of Sciences 2008); however, their megalopae are not included in our key inasmuch as they remain undescribed. Virtually no literature describing the larval and post-larval stages exists for many of the pinnotherid species found in the San Francisco Bay. Pinnotherid species known to inhabit the region are therefore grouped together in the key using one previously described morphological feature (Lough 1974). The key

was created using morphological characteristics for those megalopae of brachyurans that have been found in Bay. Illustrations, adapted from published literature or drawn from captured specimens, are provided to assist in the identification of species and of the characters used in the key. Short species descriptions are also provided within the key for all included megalopae. Along with the family Pinnotheridae, the following brachyuran megalopae are included: *Cancer productus*, *Carcinus maenas*, *Eriocheir sinensis*, *Hemigrapsus nudus*, *Hemigrapsus oregonensis*, *Lophopanopeus bellus*, *Lophopanopeus leucomanus*, *Metacarcinus anthonyi*, *Metacarcinus gracilis*, *Metacarcinus magister*, *Pachygrapsus crassipes*, *Pyromaia tuberculata*, *Rhithropanopeus harrisii*, and *Romalaeon antennarius*. The goal of this study is to supply a method of identifying the brachyuran megalopae of the San Francisco Bay Estuary system to understand better this life history stage.

It is possible that the zoeae of other brachyuran species that occupy coastal regions near San Francisco Bay (Carlton 2007; Wicksten 2009) could be transported into the Bay and metamorphose into megalopae. Because these species have yet to be reported from within the Bay, they are not included in the key (see Mooi et al. 2007; Rice and Tsukimura 2007; California Academy of Sciences 2008).

Materials and Methods

A list of brachyuran species found in San Francisco Bay was generated using the results of sampling done by researchers studying the Bay (Mooi et al. 2007; Rice and Tsukimura 2007) and the Invertebrate Collection catalog of the California Academy of Sciences (California Academy of Sciences 2008). Post-larval descriptions and illustrations were obtained for species of brachyuran crabs known to inhabit the San Francisco Bay Estuary. Literature sources used for descriptions and illustrations of megalopae are given in Table 1. Several species of Pinnotheridae are thought to inhabit San Francisco Bay, including *Pinnixa franciscana*, *P. littoralis*, *P. schmitti*, *P. occidentalis*, *P. longipes*, and *Scleroplax granulata*. Because little literature exists on the larval or post-larval description of pinnotherid crabs in the region, all the pinnotherid species have been grouped together in the key using a single morphological trait that has been previously described (Lough 1974) and used in published dichotomous keys to group species in the family Pinnotheridae (Shanks 2001).

Illustrations of megalopae for *M. gracilis*, *E. sinensis*, and the family Pinnotheridae were drawn from specimens found in light traps and zooplankton samples taken from the region. Other species illustrations used in this key were adapted from illustrations in published literature (see Table 1). Light trap sam-

TABLE 1. Sources of descriptions and illustrations for each species of Brachyuran megalopae presented in the dichotomous key.

Species	Authors
Cancer productus	Lough (1974); Trask (1970)
Carcinus maenas	Crothers (1966); Rice and Ingle (1975)
Eriocheir sinensis	Montu et al. (1996)
Hemigrapsus nudus	Hart (1935)
Hemigrapsus oregonensis	Hart (1935)
Lophopanopeus bellus	Knudsen (1959); Lough (1974)
Lophopanopeus leucomanus	Knudsen (1958)
Metacarcinus anthonyi (= *Cancer anthonyi*)	Anderson (1978)
Metacarcinus gracilis (= *Cancer gracilis*)	Ally (1975)
Metacarcinus magister (= *Cancer magister*)	Poole (1966); Lough (1974)
Pachygrapsus crassipes	Lough (1974)
Pinnotheridae	Lough (1974)
Pyromaia tuberculata	Fransozo and Negreiros-Fransozo (1997); Luppi and Spivak, (2003)
Rhithropanopeus harrisii	Connolly (1925)
Romalaeon antennarius (= *Cancer antennarius*)	Lough (1974); Roesijadi (1976)

ples were provided by the Smithsonian Environmental Research Center (Tiburon, California). Zooplankton samples were obtained from the California Department of Fish and Game *Neomysis* and Zooplankton Survey. In order to view morphological characterists clearly, specimens were preserved in 10% formalin and dyed using rose Bengal dye.

Overall, conspicuous morphological character were chosen for couplets of the dichotomous key. However, in cases where species are almost identical, less obvious morphological features are used to separate species. Illustrations are provided to make differences among species easier to detect.

A Key to Brachyuran Megalopae of the San Francisco Bay Estuary System

1A Rostrum pointed or with rostral spine (Fig. 1, arrow A) 2
1B Rostrum blunt or flat (Fig. 11A, arrow A) 9

2A Carapace with dorsal spine (Fig. 1, arrow B) Cancridae 3
2B Carapace without dorsal spine (Fig. 6, arrow A) 7

3A Carapace with reduced lateral spines (Fig. 1, arrow C) 4
3B Carapace without lateral spines (Fig. 3, arrow A) 5

4A Telson subquadrate with indentation on terminal portion (Fig. 1, arrow D) ..... *Cancer productus* Randall, 1839. (Fig. 1)

[Carapace with rostral and dorsal spines. Lateral spines on carapace greatly reduced. Carapace length about 3.6 mm. Antenna of 11 segments with proximal to distal setal arrangement of five, four, four, zero, zero, three, two, three, one, three and five, respectively. Mandible with 12 setae on palp. First Maxilliped: endopod with 38 to 40 spines on basal end and nine setae on distal end; exopod with six plumose setae on distal end. Second Maxilliped: exopod with five plumose setae. Third Maxilliped: endopod of four segments with many spines; exopod with six plumose setae. Pleon of six pleomeres plus a telson (Lough 1974; Trask 1970).]

4B Telson flat, without indentation on terminal portion (Fig. 2, arrow A) ..... *Romalaeon antennarius* (Stimpson, 1856) (= *Cancer antennarius*) (Fig. 2)

[Carapace with rostral, dorsal, and greatly reduced lateral spines. Carapace length about 2.4 mm. Antenna with 11 segments, proximal to distal setal arrangement of four, two, four, zero, zero, four, zero, five, zero, four and four, respectively. Mandible two-segmented palp with nine terminal spines. First Maxilliped: endopod of two segments. Distal segment of endopod with three subterminal plumose setae and two terminal spines; exopod of two segments with three plumose setae on proximal segment and four plumose setae on distal segment. Second Maxilliped: endopod of three segments with spine arrangement of zero, seven and eight, respectively; exopod with four plumose setae on distal segment. Third Maxilliped: endopod of four segments with spine arrangement of ten, six, eight and seven, respectively; exopod with five plumose setae on distal segment. Pleon of six pleomeres. Posterior edge of telson smooth (Lough 1974; Roesijadi 1976).]

5A Carapace length about 6.8 mm ..... *Metacarcinus magister* (Dana, 1852) (=*Cancer magister*) (Fig. 3)

[Carapace with rostral and dorsal spines. Antenna of 11 segments, proximal to distal setal arrangement of 11, 11, eight, zero, two, seven, six, two, five and five, respectively. Mandible palp with 18 spines. First Maxilliped: endopod basal end with many spines and distal end with eight to nine setae; exopod with seven terminal setae. Second Maxilliped: endopod of four segments with spine arrangement of seven, six, 20 and 14, respectively; exopod with six natatory setae on the terminal portion. Third Maxilliped: endopod of four segments with many setae on all segments. Pleon of five pleomeres plus a telson (Lough 1974; Poole 1966).]

5B Carapace length between 1.5 to 2.5 mm 6

6A Antenna of 11 (occasionally ten) segments, proximal to distal setal arrangement of five, two (occasionally three), four (occasionally three), zero, zero, four (occasionally three and five), zero, five, zero (occasionally one), four and five (Fig. 4A) and Mandibular palp with eight (sometimes seven or nine) setae on terminal segment . . . . . *Metacarcinus gracilis* (Dana, 1852) (= *Cancer gracilis*) (Fig. 4B)

[Carapace with rostral and dorsal spines. Mandible three-segmented palp with setal arrangement of zero, zero and eight, respectively. First Maxilliped: endopod flattened process with four setae; exopod of two segments with two to four plumose setae on distal portion of proximal segment and five plumose setae on terminal portion of distal segment. Second Maxilliped: endopod of five segments with setal arrangement of one, one (occasionally zero), one, six to seven (occasionally five) and nine, respectively; exopod of two segments with five plumose setae on distal segment. Third Maxilliped: endopod of five segments with setal arrangement of 23 to 27, 13 (occasionally 12), ten to 12, ten to 13 and nine, respectively; exopod of two segments with two to four setae on proximal segment and five plumose setae on second segment. Telson flat, posterior margin rounded (Ally 1975).]

6B Antenna of 11 segments, proximal to distal setal arrangement of five, two, three, zero, zero, four, zero, five, zero, five, and five (Fig. 5A) and Mandibular palp with 13 setae on terminal segment . . . . . *Metacarcinus anthonyi* (Rathbun, 1897) (=*Cancer anthonyi*) (Fig. 5B)

[Carapace with rostral and dorsal spines. Total length about 3.2 mm. First Maxilliped: endopod with 20 spines on basal portion and 15 on distal portion; exopod with five long setae on terminal portion. Second Maxilliped: endopod of four segments with spinal arrangement of two, one, seven and ten, respectively; exopod with five long setae on terminal portion. Third Maxilliped: endopod of four segments with a setal arrangement of 14, 12, 13, and ten, respectively; exopod with 15 hair-like setae along surface and six setae on terminal portion. Pleon of six pleomeres plus a telson (Anderson 1978).]

7A Telson with no terminal setae (Fig. 6, arrow B). Carapace with rostral spine . . . . . *Carcinus maenas* (Linnaeus, 1758) (Fig. 6)

[Carapace length about 1.26 to 1.4 mm. Antenna of ten segments. Mandible two-segmented palp with six terminal setae. First Maxilliped: endopod with four to five setae; exopod of two segments with setal arrangement of two, and three to five, respectively. Second Maxilliped: endopod of five segments with no setae on proximal segment; exopod of two segments with four to five setae on terminal portion of distal segment. Third Maxilliped: endopod of five segments with many setae; exopod of two segments with four setae on terminal portion of distal segment. Pleon of six pleomeres plus a posteriorly narrow telson (Crothers 1966; Rice and Ingle 1975).]

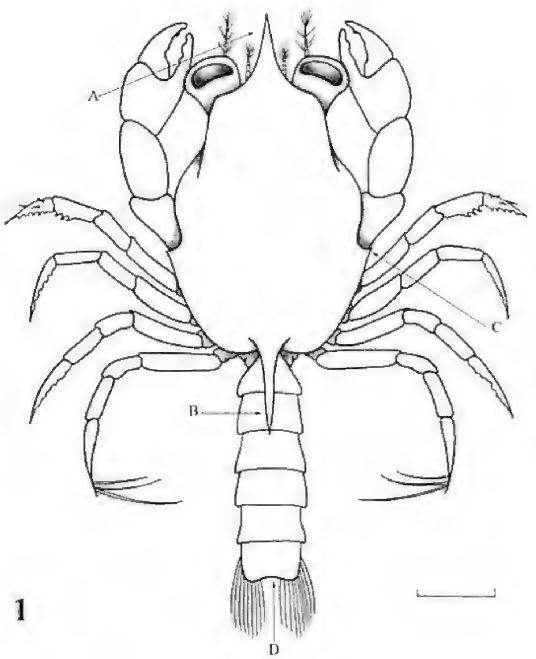
7B Telson with two or three terminal setae (Fig. 7, arrow A) 8

8A Front of carapace wide with broad rectangular projections on the antero-lateral corners (Fig. 7, arrow B) . . . . . *Lophopanopeus bellus* (Rathbun, 1900) (Fig. 7)

[Carapace with wide front, projections on the antero-lateral corners of the carapace. Carapace length about 1.68 mm. Antenna of 11 segments with cluster of setae on segments eight and ten. First Maxilliped: endopod reduced with four setae; exopod of two segments with four plumose setae on terminal portion of distal segment. Second Maxilliped: endopod of four segments with proximal to distal setal arrangement of two, zero, six and six, respectively; exopod of two segments with four setae on terminal portion of distal segment. Third Maxilliped: exopod of two segments with five setae on terminal portion of distal segment. Pleon of six pleomeres plus a telson with three terminal setae (Knudsen 1959; Lough 1974).]

8B Carapace with no rectangular projections on the antero-lateral corners of the carapace . . . . . *Pachygrapsus crassipes* Randall, 1839 (Fig. 8)

[Carapace length about 1.96 mm. Last joint of leg with three setae longer than last joint of leg. Telson with terminal two to three setae on posterior margin (Lough 1974).]



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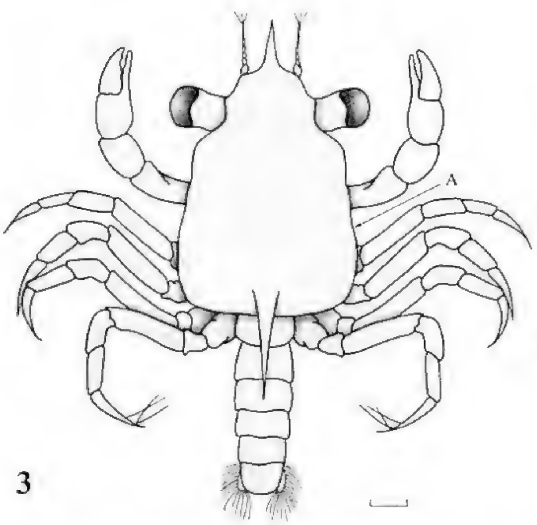

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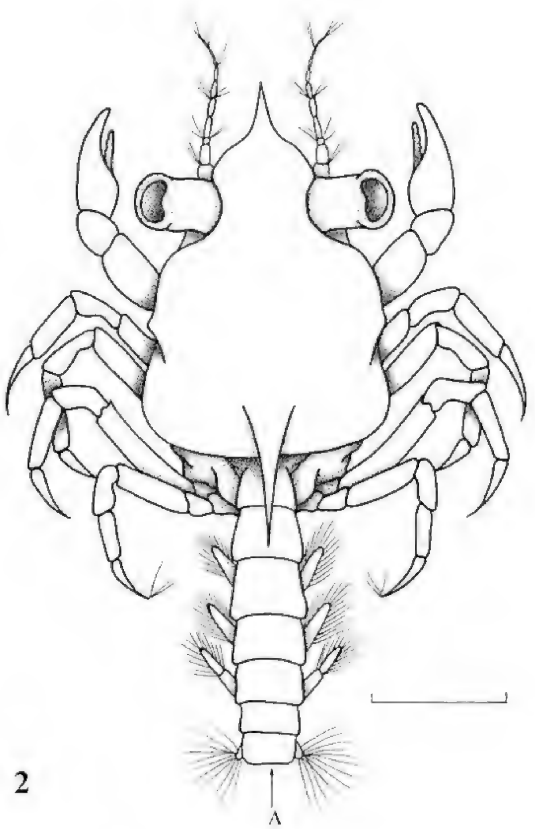
FIGURE 1. *Cancer productus* megalopa (after Trask 1970). Arrow A, Rostral spine; Arrow B, Dorsal spine; Arrow C, Reduced lateral spine; Arrow D, Telson subquadrate with indentation. Scale bar = 1 mm.

FIGURE 2. *Romalaeon antennarius* megalopa (after Roesijadi 1976). Arrow A, Telson flat without indentation. Scale bar = 1 mm.

FIGURE 3. *Metacarcinus magister* megalopa (after Poole 1966). Arrow A, Carapace without lateral spine. Scale bar = 1 mm.

FIGURE 4. (A) *Metacarcinus gracilis* antenna (after Ally 1975). (B) *Metacarcinus gracilis* megalopa (original by G.G. Castañeda). Scale bars, A = 0.1 mm; B = 1 mm.



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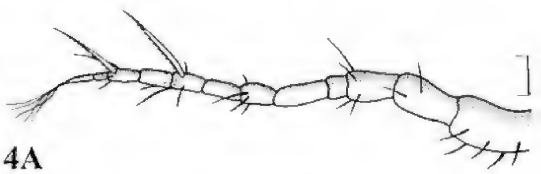

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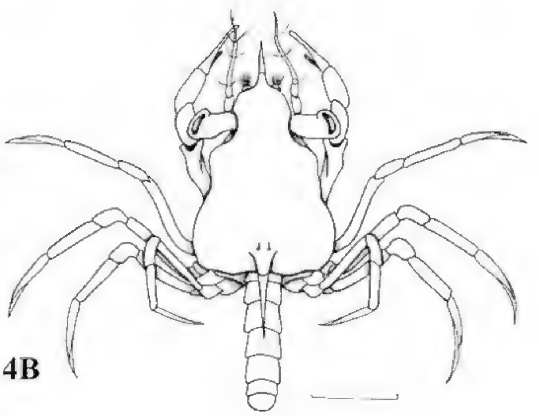

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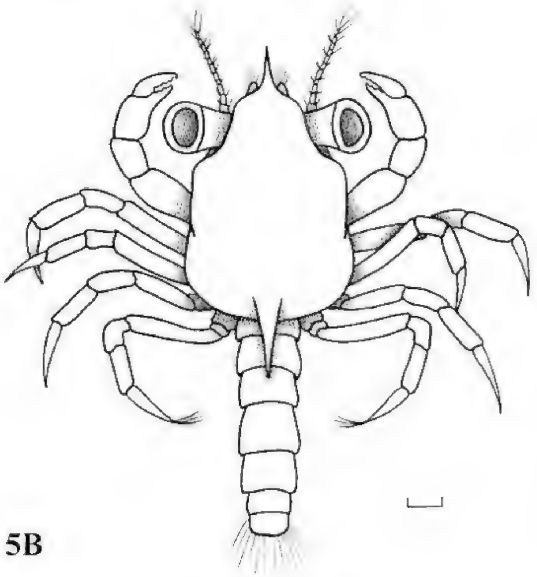


FIGURE 5. (A) *Metacarcinus anthonyi* antenna (after Anderson 1978). (B) *Metacarcinus anthonyi* megalopa (after Anderson 1978). Scale bars, A = 0.2 mm; B = 1 mm.

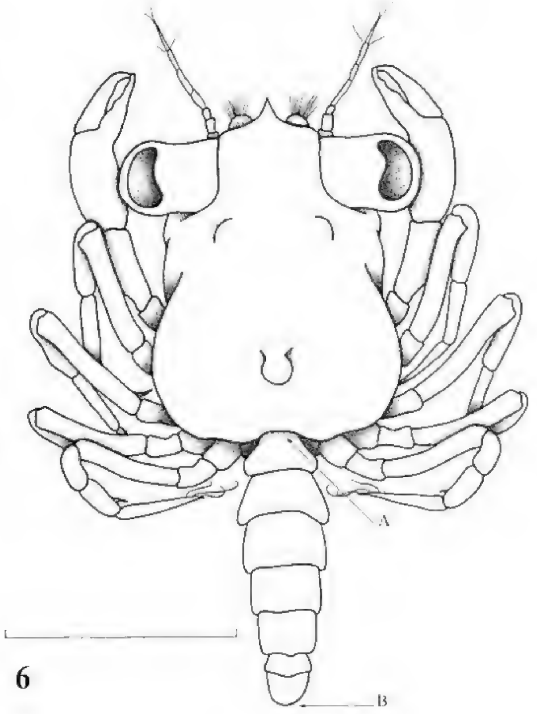


FIGURE 6. *Carcinus maenas* megalopa (after Rice and Ingle 1975). Arrow A, Carapace without dorsal spine; Arrow B, Telson without terminal setae. Scale bar = 1 mm.

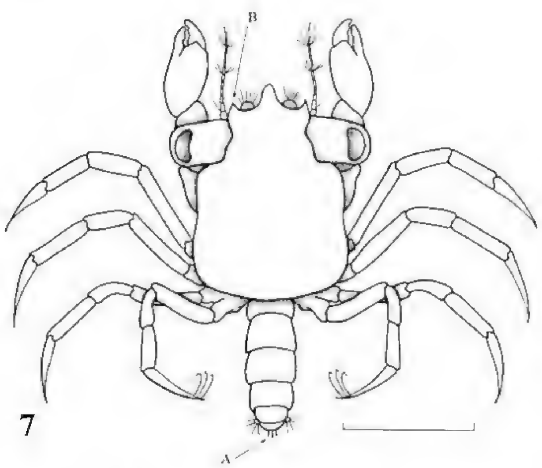


FIGURE 7. *Lophopanopeus bellus* megalopa (after Knudsen 1959). Arrow A, Telson with two or three terminal setae; Arrow B, Carapace with rectangular projections. Scale bar = 1 mm.

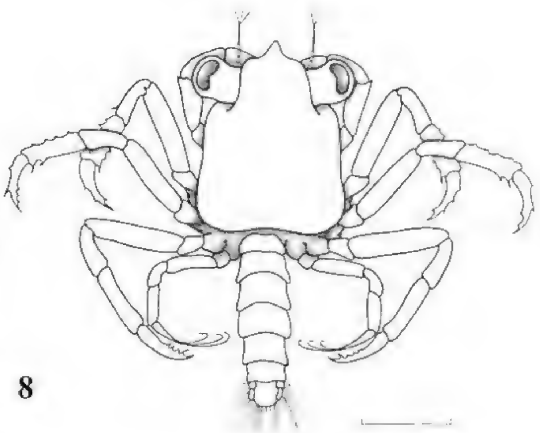
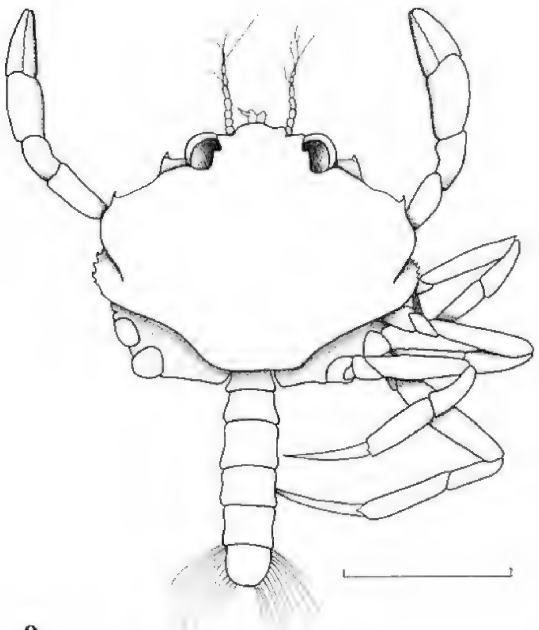


FIGURE 8. *Pachygrapsus crassipes* megalopa (after Lough 1974). Scale bar = 1 mm.

9A Width of carapace greater than length of carapace (Fig. 9). (Lough 1974) . . . .Pinnotheridae
9B Width of carapace less than length of carapace 10

10A Antenna with 11 segments 11
10B Antenna with seven to ten segments 13

11A Carapace with broad, blunt fronto-lateral projections (Fig. 10A, arrow A) . . . . .



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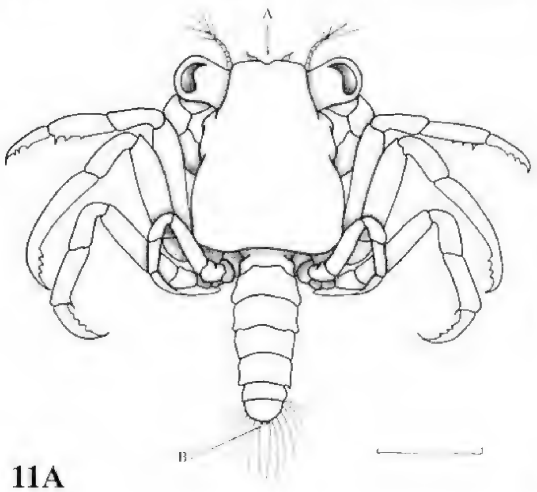
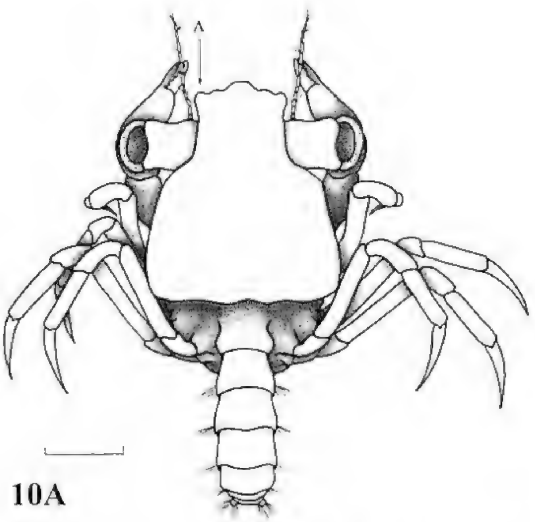
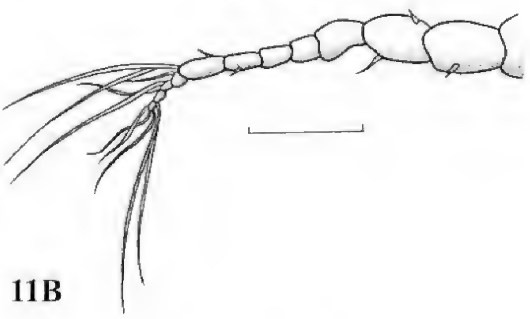
10B



11A



10A



11B

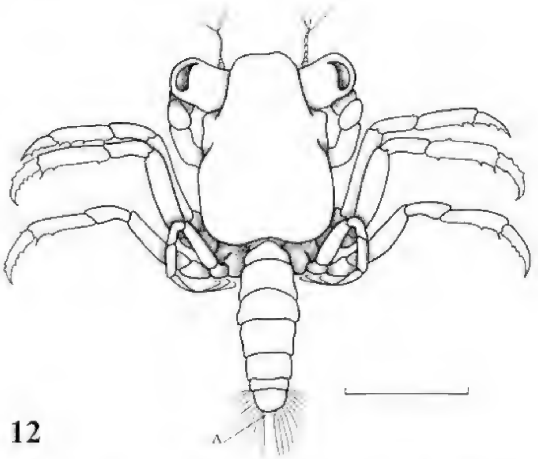


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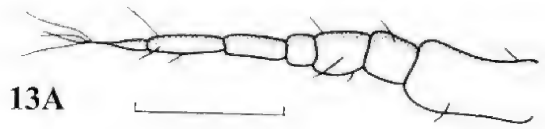
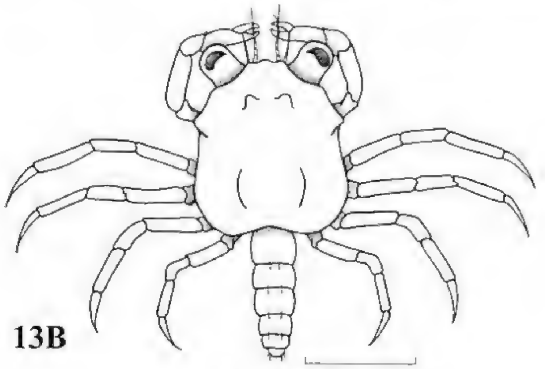
FIGURE 9. Pinnotherid megalopa (original by G. G. Castañeda). Scale bar = 1 mm.

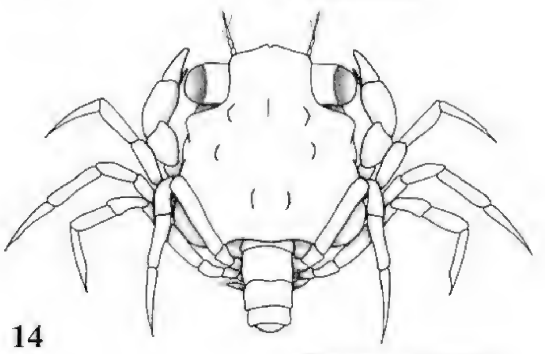
FIGURE 10. (A) *Lophopanopeus leucomanus* megalopa (after Knudsen 1958). Arrow A, Carapace with blunt frontolateral projections. (B) *Lophopanopeus leucomanus* antenna (after Knudsen 1958). Scale bars, A = 1 mm; B = 0.2 mm.

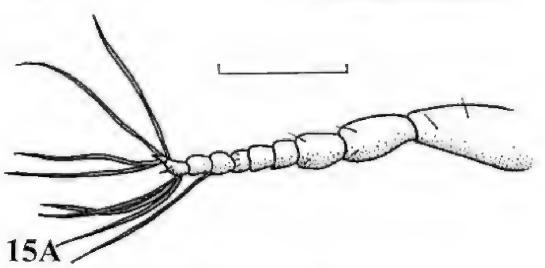
FIGURE 11. (A) *Hemigrapsus nudus* megalopa (after Hart 1935). Arrow A, Rostrum blunt or flat; Arrow B, Plumose setae on posterior margin of telson. (B) *Hemigrapsus nudus* and *Hemigrapsus oregonensis* antenna (after Hart 1935). (B). Scale bars, A = 1 mm; B = 0.175 mm.

FIGURE 12. *Hemigrapsus oregonensis* megalopa (after Hart 1935). Arrow A, No plumose setae on posterior margin of telson. Scale bar = 1 mm.









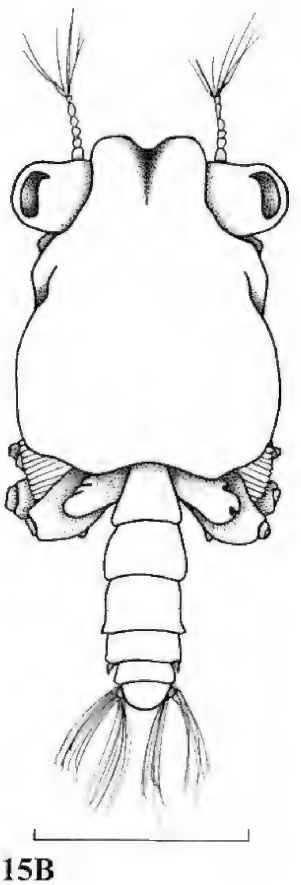


FIGURE 13. (A) *Pyromaia tuberculata* antenna (after Fransozo and Negreiros-Fransozo 1997). (B) *Pyromaia tuberculata* megalopa (after Fransozo and Negreiros-Fransozo 1997). Scale bars, A = 0.1 mm; B = 1 mm.

FIGURE 14. *Rhithropanopeus harrisii* megalopa (after Connolly 1925). Scale bar = 1 mm.

FIGURE 15. (A) *Eriocheir sinensis* antenna (after Montu et al. 1996). (B) *Eriocheir sinensis* megalopa (original by G. G. Castañeda).Scale bars, A = 0.2 mm; B = 1 mm.

[Carapace with blunt rostrum. Carapace with deep notch in frontal region. Carapace length about 1.37 to 1.55 mm. Antenna of ten segments with setal arrangement of two, two, two, zero, zero, six, one, three, three and two to three, respectively. Mandible two-segmented palp with setal arrangement of zero, and eight to nine, respectively. First Maxilliped: endopod with 15 setae; exopod of two segments with setal arrangement of one to two, and eight to nine, respectively. Second Maxilliped: endopod of four segments with setal arrangement of four, zero, five and 13, respectively; exopod of two segments with setal arrangement of zero and nine, respectively. Third Maxilliped: endopod of four segments with setal arrangement of 11, six, eight, and seven, respectively; exopod of two segments with setal arrangement of zero and four, respectively. Pleon of six pleomeres with postero-lateral spines on the second, third and fourth segment. Telson subquadrate with rounded edges (Montu et al. 1996).]

Acknowledgments

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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The California Academy of Sciences Gulf of Guinea Expeditions (2001, 2006, 2008) VII. Acanthaceae of São Tomé and Príncipe

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In this floristic study, 13 genera with 16 species of Acanthaceae are treated as native to the island nation of São Tomé and Príncipe in the Gulf of Guinea: *Acanthus montanus*, *Asystasia gangetica*, *Avicennia germinans*, *Brachystephanus occidentalis*, *Brillantaisia lamium*, *B. owariensis*, *B. vogeliana*, *Dicliptera verticillata*, *Elytraria marginata*, *Heteradelphia paulowilhelmia*, *Justicia tenella*, *J. thomensis*, *Nelsonia smithii*, *Phaulopsis micrantha*, *Rhinacanthus virens*, and *Stenandriopsis thomensis*. Three species (*Brachystephanus occidentalis*, *Heteradelphia paulowilhelmia*, and *Justicia thomensis*) are endemic to São Tomé. Fourteen of the native species occur on São Tomé and nine species occur on Príncipe. An additional species (*Ruellia brevifolia*) from South America is naturalized on São Tomé. This account includes keys to and descriptions of all native and naturalized taxa, information on phenologies and distributions, conservation notes for rare and endemic species, and taxonomic and/or morphological notes as appropriate.

Neste estudo florístico, 13 géneros e 16 espécies de Acanthaceae são considerados nativos em São Tomé e Príncipe: *Acanthus montanus*, *Asystasia gangetica*, *Avicennia germinans*, *Brachystephanus occidentalis*, *Brillantaisia lamium*, *B. owariensis*, *B. vogeliana*, *Dicliptera verticillata*, *Elytraria marginata*, *Heteradelphia paulowilhelmia*, *Justicia tenella*, *J. thomensis*, *Nelsonia smithii*, *Phaulopsis micrantha*, *Rhinacanthus virens*, e *Stenandriopsis thomensis*. Três espécies (*Brachystephanus occidentalis*, *Heteradelphia paulowilhelmia*, e *Justicia thomensis*) são endémicas em São Tomé. Catorze espécies indígenas ocorrem em São Tomé e nove no Príncipe. Uma espécie adicional (*Ruellia brevifolia*) originária da América do Sul, encontra-se naturalizada em São Tomé. Esta revisão inclui chaves e descrição de todos os táxones nativos e naturalizados, informação sobre fenologia e distribuição, notas sobre conservação de espécies raras e endémicas, e notas taxonómicas e/ou morfológicas relevantes.

Introduction

Recent phylogenetic studies of Acanthaceae based primarily on DNA sequence data reveal that Africa is likely the ancestral source area for major lineages and genera of the family (e.g., Daniel et al. 2008; Tripp 2008; Borg et al. 2008; Wenk and Daniel 2009). Therefore knowledge of the family in and around this continent is essential for understanding its phylogenetic and biogeographic

histories. In this study we present a taxonomic account of the family in the nation of São Tomé and Príncipe, which comprises two islands in the Gulf of Guinea (Fig. 1).

The four major islands in the Gulf of Guinea are all volcanic in origin and lie along the Cameroon Line, a linear zone of weakness in the earth's crust along which Mt. Cameroon and the Cameroon highlands also occur on the African continent. The islands vary in age, size, distance from the mainland, elevation, past connections to the mainland (i.e., continental vs. oceanic islands), and species compositions. Table 1 summarizes some of the principle features of the islands and the numbers of Acanthaceae on each. Appendix I lists the acanthaceous flora of each of the major islands in the Gulf of Guinea. Due to its larger size, greater elevational range, and proximity to/past connections with the African mainland, Bioko is the most species-rich of the islands, but it also exhibits a relatively low level of endemism. The three oceanic islands of this tropical archipelago show a richness of Acanthaceae that is positively correlated with relative size and elevational ranges of the islands. Exell (1944, 1973) and Figueiredo (1994) studied the floras of the islands in the Gulf of Guinea and concluded that: the flora of Bioko is more similar to that of the African mainland (to which it was previously attached) than to the other (oceanic) islands; the floras of the oceanic islands appear to have originated independently and solely by dispersal; neighboring islands tend to have high floristic affinities; and Acanthaceae are one of the most taxon-rich families occurring there.

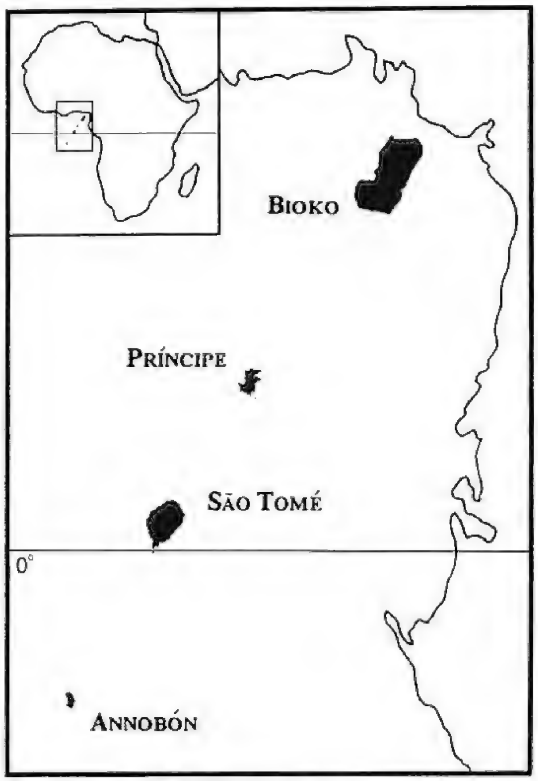

FIGURE 1. Location of the Gulf of Guinea and the major islands there.

TABLE 1. Some comparative statistics of the major islands in the Gulf of Guinea.

Characteristic	Bioko	Príncipe	São Tomé	Annobón
Area (sq. km)	2017	128	836	17
Age (mybp)	1.1	31	13	5
Highest Elevation (m)	3012	948	2024	598
Distance from Africa (km)	32	210	235	340
Acanthaceae (native species)	46	9	14	3

Some of the most useful previously published studies that deal extensively with the Acanthaceae of São Tomé and Príncipe (as well as other islands in the Gulf of Guinea) are the annotated floristic lists of Exell (1944, 1973), who also discussed the important historical collectors who visited the islands, and irregularities in the numbering of duplicates of collections of Moller and Quintas (Exell 1944); Heine's (1966) treatment of Acanthaceae in the *Flore du Gabon,* which includes many of the same species, often with illustrations; and Heine's (1963) account of Acanthaceae in the second edition of the *Flora of West Tropical Africa.*

In our study 13 genera with 16 species of Acanthaceae are treated as native to the nation of

São Tomé and Príncipe. Although none of the genera is endemic to these islands, three of the species (*Brachystephanus occidentalis*, *Heteradelphia paulowilhelmia*, and *Justicia thomensis*; 19% of the total native species) are. Eleven of the genera and 14 of the species occur on São Tomé while nine species in nine genera occur on Príncipe (Appendix I). All three of the endemic species are restricted to the larger island of São Tomé. The two species occurring on Príncipe that are not known from São Tomé are *Acanthus montanus* and *Rhinacanthus virens*. Other than the three species endemic to São Tomé, the following species are known from São Tomé, but not from Príncipe: *Avicennia germinans*, *Brachystephanus occidentalis*, *Brillantaisia owariensis*, *B. vogeliana*, and *Phaulopsis micrantha*.

Except for *Avicennia*, which has embryos readily capable of oceanic dispersal (Tomlinson 1986), most Acanthaceae are commonly absent or rare on isolated oceanic islands (e.g., Hawaii, Galápagos Islands). Because of their general lack of morphological characteristics that might promote long distance dispersal, rafting appears to be the most plausible explanation for dispersal of Acanthaceae across significant water barriers (e.g., Wenk and Daniel 2009). However, most Acanthaceae tested to date (Daniel 1993 and unpublished) are both autogamous and self-compatible. Thus, upon dispersal, many Acanthaceae would have a reasonably good chance of establishment. It is likely that most of the Acanthaceae native to São Tomé and Príncipe arrived on the islands via rafting of mats of vegetation originating in the major rivers of western Africa and were carried there by a combination of the Guinea, Congo (Benguella), and South Equatorial currents (see Measey et al. 2007). Because some species (e.g., *Brillantaisia* spp., *Justicia tenella*, *Phaulopsis micrantha*) have seeds bearing hygroscopic/mucilaginous trichomes, which might become attached to birds, it is also possible that avian dispersal might have played a role in dispersal of some species to the islands.

In addition to the 16 species that are known or presumed to be native to São Tomé and Príncipe, the introduced South American *Ruellia brevifolia* has become established on São Tomé and is treated as naturalized there. Like most Acanthaceae it is self-compatible, sets abundant fruit, and spreads by seeds. Numerous Acanthaceae are cultivated for ornament on one or both islands, including *Acanthus montanus* (native; see below), *Brachystephanus occidentalis* (native; see below), *Fittonia albivenis* (Lindl. ex Veitch) Brummitt (native to South America; decumbent herbs with conspicuous yellowish veins in the leaves and small yellowish flowers in pedunculate spikes), *Graptophyllum pictum* (L.) Nees ex Griff. (native to Indo-Pacific islands; shrubs with conspicuously multi-colored leaves and relatively large, maroon colored flowers), *Hemigraphis* sp. (possibly *H. reptans* (G. Forst.) T. Anders., which is native to Pacific islands; herbs with foliage nearly black and with subactinomorphic white corollas in densely bracteate spikes), *Justicia secunda* Vahl (native to tropical America; a tall shrub with red and strongly 2-lipped corollas), *Ruellia simplex* Wright (= *R. coerulea* Morong and *R. tweediana* Griseb.; native to the New World; a perennial herb to shrub with very narrow and elongate leaves, and with large funnelform blue flowers), *Sanchezia parvibracteata* (native to the New World; a shrub with coriaceous leaves that have white to yellowish veins, and with spikes of tubular and yellow flowers subtended by coarse, basally fused bracts), *Thunbergia alata* Boj. ex Sims (native to Africa; a vine with sagittate leaf blades borne on a winged petiole and with subactinomorphic corollas that are usually orange with a dark spot at the mouth), and *T. grandiflora* (native to Asia; a liana with large, subactinomorphic, and blue or white corollas subtended by two ± coherent spathaceous bracteoles) . Some of these may persist after cultivation or sometimes escape to disturbed habitats (e.g., *Thunbergia alata*). However, none of these is known to have become established to the extent of *R. brevifolia*.

Figueiredo (1994) noted the lack of collections (especially of endemic taxa) in the islands in the Gulf of Guinea, and the need for additional botanical inventory there. Portions of both islands

under consideration here remain to be adequately explored and collected, including southern and western São Tomé and southern Príncipe. Additional species of Acanthaceae likely either occurred or will be found in São Tomé and Príncipe. In addition to the species treated in this account, Exell (1944) noted a collection from São Tomé (without locality, *G. Don s.n.* at BM) that he indicated probably represents an undescribed species of *Hypoestes* but which lacked sufficient material for characterization (see Milne-Redhead in *Bull. Misc. Inf. Kew* 1940:64. 1940, who noted that Don's specimen is distinct from *H. consanguinea* Lindau and *H. rosea* Beauv.). Another collection (possibly *Hypoestes*, but lacking flowers or fruits) from São Tomé was acquired more recently (*F. de Oliveira 944* at BRLU). Exell (1944) also noted that a collection of Chevalier (no. *14563* from between Monte Café and the Pico) had been cited as an unidentified genus of Acanthaceae. The identities of these plants will require additional studies and/or collections.

Materials and Methods

Keys and descriptions in the following taxonomic account are based only on plants from São Tomé and Príncipe (except as noted). We presume to have studied most of the known collections of Acanthaceae from the islands. In addition to our own collections, we studied those in most of the herbaria that house significant materials from São Tomé and Príncipe (BRLU, COI, K, LISC, LISU, STPH). We were unable to study most specimens at BM because they were inaccessible during renovation of that herbarium. However, many of the collections there are duplicated at other herbaria whose specimens we studied. We were also unable to study some recent collections of Jorge Paiva at COI and Faustino de Oliveira at BRLU and STPH because they were unprocessed and unavailable during our study. Because of the primarily taxonomic nature of this account, the conservation status of each species according to the IUCN Red List Criteria (IUCN 2009) could not be determined. Instead, for species that might be of concern due to their apparent rarity or endemicity, we offer anecdotal comments relating to their conservation status based on the information presented or available. The known synonymy of all taxa is either provided or referenced. Full nomenclatural information for synonyms is provided only for names based on collections from São Tomé and Príncipe. Original photographic images of most of the species native to São Tomé and Príncipe (Figs. 2–4) as well as SEM images of pollen of most species (Figs. 5–7) are provided.

Taxonomic Account

Acanthaceae

Terrestrial (rarely aquatic) annual to perennial herbs or shrubs, less often trees or twining perennial vines, vegetative and floral organs glabrous or pubescent with various types of eglandular (simple and compound), subglandular (i.e., lacking a conspicuous capitate gland at apex but apically enlarged), and glandular trichomes, often covered with cystoliths visible in epidermis (these absent in some genera); young stems usually with swollen nodes. Leaves opposite and decussate or sometimes whorled (rarely alternate), simple, estipulate, sessile to petiolate, margin entire, less often crenate to dentate. Inflorescence of 1–many-flowered dichasia borne in axils of leaves or bracts; dichasia alternate (= solitary) or opposite (= paired) at nodes, sessile or pedunculate, when borne in axils of bracts then usually forming dichasiate spikes (i.e., dichasia and flowers sessile to subsessile), racemes (i.e., dichasia sessile to subsessile and flowers pedicellate), or thyrses (i.e., dichasia pedunculate), if spikes or racemes or thyrses branched then forming panicles, bracts subtending dichasia large and brightly colored or small and green. Flowers sessile or pedicellate, usually subtended by 2 bracteoles, bisexual, chasmogamous and sometimes cleistogamous as well,

rarely heterostylous. Calyx comprising 5 sepals, free or usually fused and deeply 4–5-lobed, lobes equal to unequal in length, sometimes partially or completely fused with one another and forming heteromorphic segments. Corolla sympetalous, comprising 5 petals, tube cylindric or funnelform (i.e., gradually or abruptly expanded distally into a ± distinct throat), sometimes resupinate, limb subactinomorphic or usually 2-labiate with an upper lip of 2 lobes and a lower lip of 3 lobes, corolla lobes imbricate (including cochlear and quincuncial) or contorted in bud. Stamens epipetalous, included in corolla tube or exserted from mouth of corolla, usually 2 or 4 and didynamous; anthers 1–2-thecous, sometimes with basal or apical appendages, thecae of a pair parallel to perpendicular, collaterally attached to filament to superposed to widely separated by a modified connective, pollen extremely diverse; staminodes 0–3; pollen diverse. Nectariferous disk usually present around base of ovary, annular. Gynoecium 2-carpellate; ovary superior, generally 2-locular, placentation usually axile, ovules 2–many in each locule; style simple, terminal, filiform, included within corolla tube or exserted from mouth of corolla; stigma funnelform, 2-lobed, or with one lobe suppressed. Fruit a loculicidal, explosively dehiscent, stipitate or estipitate, 2-valved indurate capsule (rarely a fleshy drupe or leathery capsule), septa sometimes separating elastically from inner wall of mature capsule. Seeds 2–many per valve, each usually subtended by a prominent hook-shaped retinaculum, usually discoid to globose, glabrous or pubescent, trichomes often hygroscopic or becoming mucilaginous when wet. ($x = 7$).

Most of the ca. 4000 species occur in the tropics and subtropics with major centers of endemism, morphological diversity, and species richness in Indo-Malesia, Africa (including Madagascar), South America, and Mexico-Central America. Plants occur in most tropical habitats except those at very high elevations (i.e., above 3000 meters). Sixteen species in 13 genera are here treated as native to São Tomé and Príncipe. An introduced species in an additional genus (*Ruellia brevifolia*) is widely naturalized on São Tomé. These 17 species can be distinguished by the following key and the keys to species of *Brillantaisia* and *Justicia* under treatments of those genera below. Other species that are cultivated in the islands and may sometimes persist or escape are noted above.

Key to Acanthaceae of São Tomé and Príncipe

1. Shrubs or trees with leathery (entire and not spiny) leaves, occurring along or near shores; erect aerial roots (pneumatophores) up to 3 dm tall present in vicinity of plants; capsule leathery, lacking retinacula, containing 1 (–2) seeds ..... *Avicennia germinans*
1. Herbs or shrubs usually with membranaceous leaves (if the leaves chartaceous, as in *Acanthus montanus*, then with at least some, most, or all of them pinnately lobed and spiny), occurring near shores and elsewhere; erect aerial roots (pneumatophores) absent; capsule indurate when mature, with or without retinacula, usually containing more than 2 seeds.
    2. Plants lacking conspicuous linear crystals (cystoliths) in epidermis of stems and leaves; corolla lobes with descending-cochlear aestivation; capsules lacking hooklike retinacula subtending seeds.
        3. Plants erect, not rooting at nodes; leaves in 1–3 (or more?) clusters or whorls along and/or at apex of stems, (3–) 6–11 per node; peduncle of inflorescence covered with spirally arranged, remote and sparse, conduplicate-clasping scales; spikes 4–8 mm in diameter near midpoint; bracts mucronate at apex (mucro to 1 mm long); flowers subtended by 2 bracteoles; corolla entirely cream-white ..... *Elytraria marginata*
        3. Plants mostly trailing, rooting at nodes; leaves opposite, ± evenly distributed along stems, 2 per node; peduncle (if present) of inflorescence naked (lacking scales); spikes

8–12 mm in diameter near midpoint; bracts not mucronate at apex; flowers not subtended by 2 bracteoles; corolla white with pink on lobes . . . . . *Nelsonia smithii*

2. Plants with or without cystoliths in epidermis of stems and leaves; corolla lobes with other types of aestivation; capsules with conspicuous hooklike retinacula subtending seeds.
   4. Plants lacking cystoliths in epidermis of stems and leaves; stamens 4, anthers 1-thecous; pollen 3-colpate.
      5. Leaves chartaceous, margin (entire to dentate to) pinnatisect with lobes 7–31 mm deep, secondary veins extending beyond margin of lobes as sharp spines to 4 mm long; calyx deeply 4-lobed, 27–33 mm long, lobes heteromorphic; corolla white with pinkish to maroon veins, 40–48 mm long, tube very short (5–7 mm long), limb 1-labiate, consisting of a 3-lobed lower lip; stamens exserted from corolla tube, 20–23 mm long, anthers 10–11 mm long . . . . . *Acanthus montanus*
      5. Leaves membranaceous, margin entire to sinuate; calyx deeply 5-lobed, 14–18 mm long, lobes ± homomorphic; corolla blue, lilac, or purplish, 32–40 mm long, tube 20–26 mm long, limb 2-labiate, upper lip 2-lobed, lower lip 3-lobed; stamens included in corolla tube, 4 mm long, anthers 2.4–3 mm long . . . . . *Stenandriopsis thomensis*
   4. Plants with conspicuous cystoliths in epidermis of stems and leaves; stamens either 2 (anthers 1-or 2-thecous) or 4 (anthers 2-thecous); pollen not 3-colpate.
      6. Stamens 4.
         7. Leaves at a node mostly anisophyllous; corolla white (lacking colored markings), 4.2–5 mm long; capsule 4–5 mm long, septa with attached retinacula separating from inner wall of mature capsule . . . . . *Phaulopsis micrantha*
         7. Leaves at a node mostly isophyllous; corolla white (with colored markings within), blue, violet, purple, maroon, or red, (11–) 13–79 mm long; capsule 12–31 mm long, septa with attached retinacula remaining attached to inner wall of mature capsule.
            8. Limb of corolla strongly zygomorphic, upper lip conduplicate-hooded, enclosing stamens; pollen 4-colporate; capsule estipitate; seeds covered with hygroscopic trichomes . . . . . *Brillantaisia*
            8. Limb of corolla weakly zygomorphic to subactinomorphic, upper lip neither conduplicate-hooded nor enclosing stamens; pollen 3-porate to 3-colporate; capsule substipitate to stipitate; seeds with conspicuous hygroscopic trichomes absent, not evident, or restricted to margin.
               9. Corolla white with maroon markings within, 13–24 mm long, lobes ascending-cochlear in bud; stamens included in corolla tube; pollen 3-colporate; seeds up to 2 per capsule valve . . *Asystasia gangetica*
               9. Corolla maroon-purple to purple-violet or red, 30–79 mm long, lobes contorted in bud; stamens at least partially exserted from mouth of corolla; pollen 3-porate; seeds up to 7 per capsule valve.
                  10. Corolla maroon-purple to purple-violet, 65–79 mm long; flowers subsessile to short pedicellate, pedicels to 2 mm long; calyx 19–27 (or longer in fruit) mm long; thecae 3–4.9 mm long; capsule substipitate, linear-ellipsoid; conspicuous hygroscopic trichomes not evident on seeds; native plants occurring in montane forests above 1000 m . . . . . *Heteradelphia paulowilhelmia*
                  10. Corolla red, 30–35 mm long; flowers pedicellate, pedicels 3–7

(–11) mm long; calyx 7–11 mm long; thecae 1.7–1.9 mm long; capsule stipitate, obovoid to clavate; seeds with a conspicuous band of hygroscopic trichomes restricted to the margin; introduced plants occurring in second growth and disturbed areas below 700 m ..... *Ruellia brevifolia*

6. Stamens 2.
   11. Anthers 1-thecous; corolla 15–29 mm long; stamens 12–18 mm long, thecae 1.5–2.3 mm long ..... *Brachystephanus occidentalis*
   11. Anthers 2-thecous; corolla 2.6–16 (–17 mm long); stamens 1.5–5.5 (–9) mm long, thecae 0.2–1 (–1.7) mm long.
      12. Inflorescence of cymes of cymules, cymules comprising an involucre of several pairs of bracteoles, outer pair subequal to unequal in size, conspicuously venose; corolla resupinate (at least 90°) with the tube twisted, upper lip not rugulate (i.e., lacking a stylar furrow); septa with attached retinacula separating and rising from inner wall of mature capsule .... *Dicliptera verticillata*
      12. Inflorescence not as above; corolla not resupinate (tube not twisted), upper lip rugulate (i.e., with a stylar furrow); septa with attached retinacula not separating from inner wall of mature capsule.
         13. Corolla tube narrow and cylindric, at least twice as long as limb .. .. *Rhinacanthus virens*
         13. Corolla tube funnelform (i.e., expanded toward apex), shorter than or as long as limb ..... *Justicia*

Acanthus L., Sp. Pl. 639. 1753.

LECTOTYPE (designated by Green, Prop. Brit. Bot. 170. Aug 1929).— *Acanthus mollis* L.

Dilivaria Juss., Gen. Pl. 103. 1789.
Acanthodus Raf., Princ. Fond. Somiol. 25. 1814 ("1813").
Cheilopsis Moq.-Tand., Ann. Sci. Nat. (Paris) 27:230. 1832.
Zonablephis Raf., Sylva Tell. 143. 1838.

Perennial herbs or shrubs or (rarely) trees lacking cystoliths. Leaves opposite, in whorls of 4, or in a basal cluster, entire to deeply divided, often spiny. Inflorescence in ± dense terminal dichasiate spikes; dichasia 1-flowered; flowers usually subtended by 2 bracteoles. Calyx of 4 free sepals, the upper and lower much larger than laterals. Corolla white, purple, or pink, tube very short, limb of a single (lower) lip, lip 3(–5)-parted, corolla lobes ascending-cochlear (or aestivation open) in bud. Stamens 4, exserted from corolla tube; filaments bony; anthers 1-thecous, densely bearded, lacking basal appendages; pollen 3-colpate; staminodes 0. Capsule estipitate, ellipsoid to ovoid, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic). Seeds 2 (or fewer by abortion) per valve, discoid, with or without trichomes.

Some 20–25 species occur in the Old World tropics and subtropics (southern Europe, Africa, Asia, Malesia, and Australia); numerous species are cultivated for ornament worldwide. The genus pertains to subfamily Acanthoideae, tribe Acantheae (McDade et al. 2005).

Acanthus montanus (Nees) T. Anders., J. Proc. Linn. Soc., Bot. 7:37. 1863 ["1864"]. *Cheilopsis montana* Nees in Alph. de Candolle, Prodr. 11:272. 1847. TYPE.— EQUATORIAL

GUINEA. Bioko ("Fernando Po"): "in montibus vulgaris, Novembri" (fide protologue), *Vogel s.n.* (holotype: K ex hb. Hooker).

Perennial herbs or shrubs to 7 (–10) dm tall, sometimes rooting at nodes (nodal roots sometimes aerial); young stems ± glabrous or pubescent (especially near nodes) with flexuose eglandular trichomes 0.7–1.3 mm long. Leaves opposite, chartaceous, petiolate, petioles (4–) 8–25 mm long, blade elliptic to obovate and usually ± deeply pinnately lobed, 35–290 mm long, 18–106 mm wide, 1.8–3.2 × longer than wide, (rounded-emarginate to) long-attenuate at apex, acute to attenuate at base, surfaces sparsely pubescent (especially along major veins) with eglandular trichomes 0.1–1.5 mm long, margin (entire to dentate to) pinnatisect with lobes 7–31 mm deep, secondary veins extending beyond margin of lobes as sharp spines to 4 mm long. Spikes (including peduncle, if present) to 19 cm long, 6.5 cm in diameter (measured flat) near midspike, rachis evenly pubescent with retrorse to retrorsely appressed eglandular trichomes 0.1–0.3 mm long. Bracts opposite, often with some maroon coloration distally, elliptic to obovate, 26–38 mm long, 20–32 mm wide, attenuate and spinose at apex, abaxial surface evenly pubescent with ± erect eglandular trichomes 0.05–0.2 mm long, margin pinnate-pectinately lobed, lobes prominently spinose, 3–10 mm deep, spines to 3.5 mm long. Bracteoles linear-elliptic, 21–26 mm long, 3–5.5 mm wide, margin distally spinose-dentate, abaxial surface pubescent like bracts. Calyx 27–33 mm long, posterior and anterior lobes largest, linear-elliptic to ± oblanceolate, 27–33 mm long, margin distally spinose-dentate, lateral lobes ovate-lanceolate to lanceolate, 17–18 mm long, margin entire. Corolla white with pinkish to maroon coloration in veins, 40–48 mm long, externally (i.e., abaxially) pubescent with erect to flexuose to retrorse glandular and eglandular trichomes 0.05–0.2 mm long, tube 5–7 mm long, lower lip obovate, lobes 6–7 mm long, 12–13.5 mm wide. Stamens 20–23 mm long; filaments proximally pubescent with erect glandular trichomes to 0.05 mm long (glandular puberulent); thecae 10–11 mm long, glandular puberulent and densely pubescent with bristlelike eglandular trichomes to 2 mm long; pollen (fig. 5A) 3-colpate, interapertural surfaces reticulate. Style 24 mm long; stigma equally 2-lobed, lobes 0.6–0.7 mm long. Capsule not seen. Figure 2A–B.

Illustrations.— Heine (1963:411, fig. 302); Heine (1966:113, fig. 23).

Phenology.— Flowering: November–April, July; fruiting: unknown in São Tomé and Príncipe.

Distribution and habitat.— Native to Africa (Angola, Benin, Cameroon, Central African Republic, Congo-Kinshasa, Equatorial Guinea [Bioko], Gabon, Nigeria, São Tomé and Príncipe, Sierra Leone). This species is widely cultivated worldwide and has become naturalized in some tropical regions (e.g., Mauritius [Bosser & Heine 2000]). It appears to be native to Príncipe where plants occur in swales (wet or seasonally flooded) and along streams or trails in moist to wet lowland and montane forests at elevations from sea level to 250 m. It is likely only cultivated (or also possibly escaped) on São Tomé where it occurs in cultivated lands (including the botanical garden at Bom Sucesso).

Local names.— "Castanheiro-de-São-Tomé" (Figueiredo 2002), "cundú-de-muala-vé" (Figueiredo 2002).

Ethnobotany.— Infusions of the leaves are used in São Tomé to treat asthma and abdominal pains (Sequeira 1994).

Notes.— Entire- to nearly entire-margined leaves are rare and occur (usually proximally) on the same individuals with pinnately lobed leaves.

The name "Acanthus tetragonus R.Br.," which was cited by Nees in the protologue of *Cheilopsis montana* was not validly published by Brown, and pertains to *Blepharis edulis* (Forssk.) Pers. (Vollesen 2000).

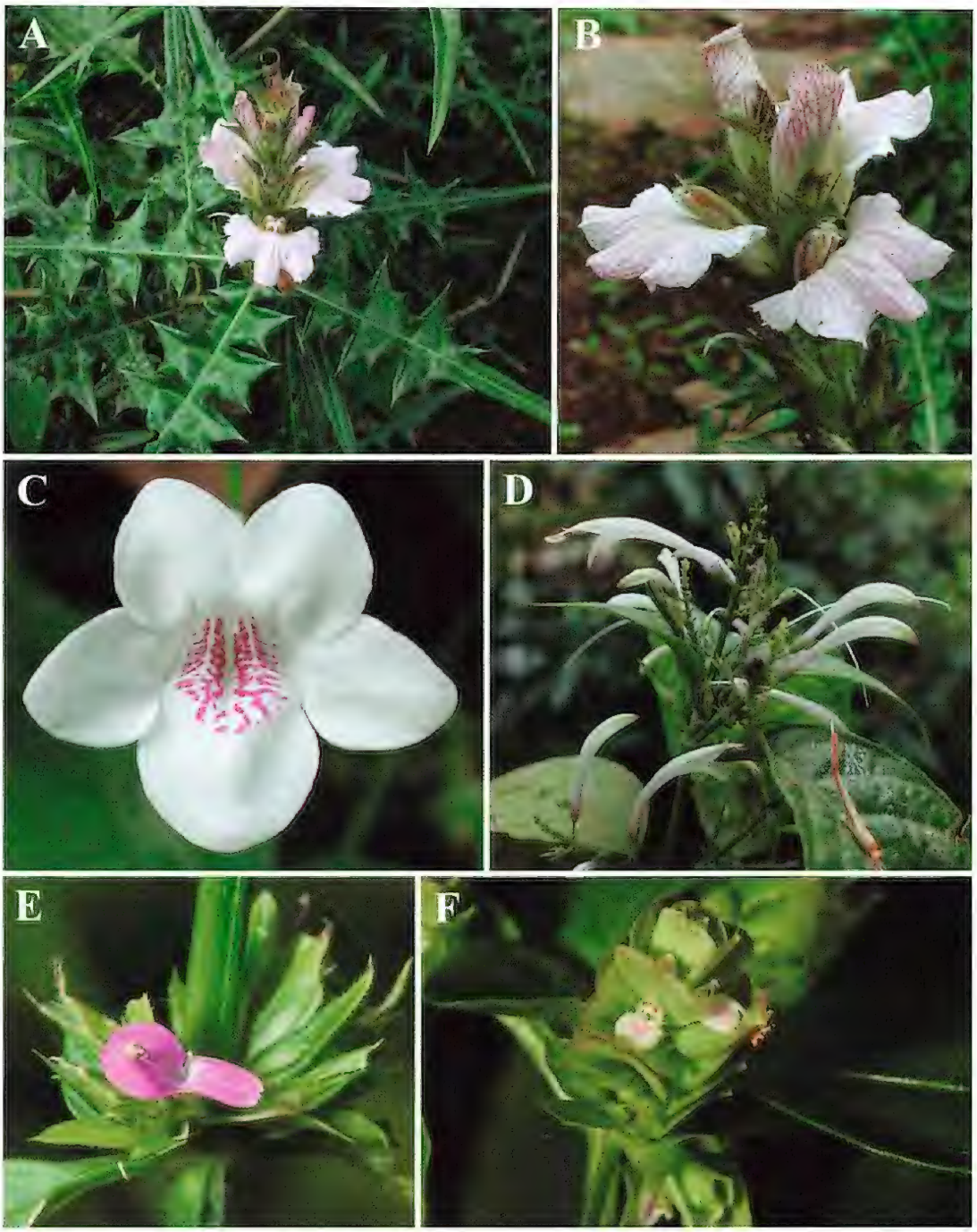

FIGURE 2. Acanthaceae of São Tomé and Príncipe. A. *Acanthus montanus*, habit (plant cultivated at Jardim Botânico de Bom Sucesso). B. *Acanthus montanus*, inflorescence (plant cultivated at Jardim Botânico de Bom Sucesso). C. *Asystasia gangetica*, flower (*Daniel 11191*). D. *Brachystephanus occidentalis*, inflorescence (plant cultivated at Jardim Botânico de Bom Sucesso). E. *Dicliptera verticillata*, inflorescence (*Daniel 11122*). F. *Justicia tenella*, inflorescence (*Daniel 11179*). Photos by T. Daniel except E and F by W. Eekerman.

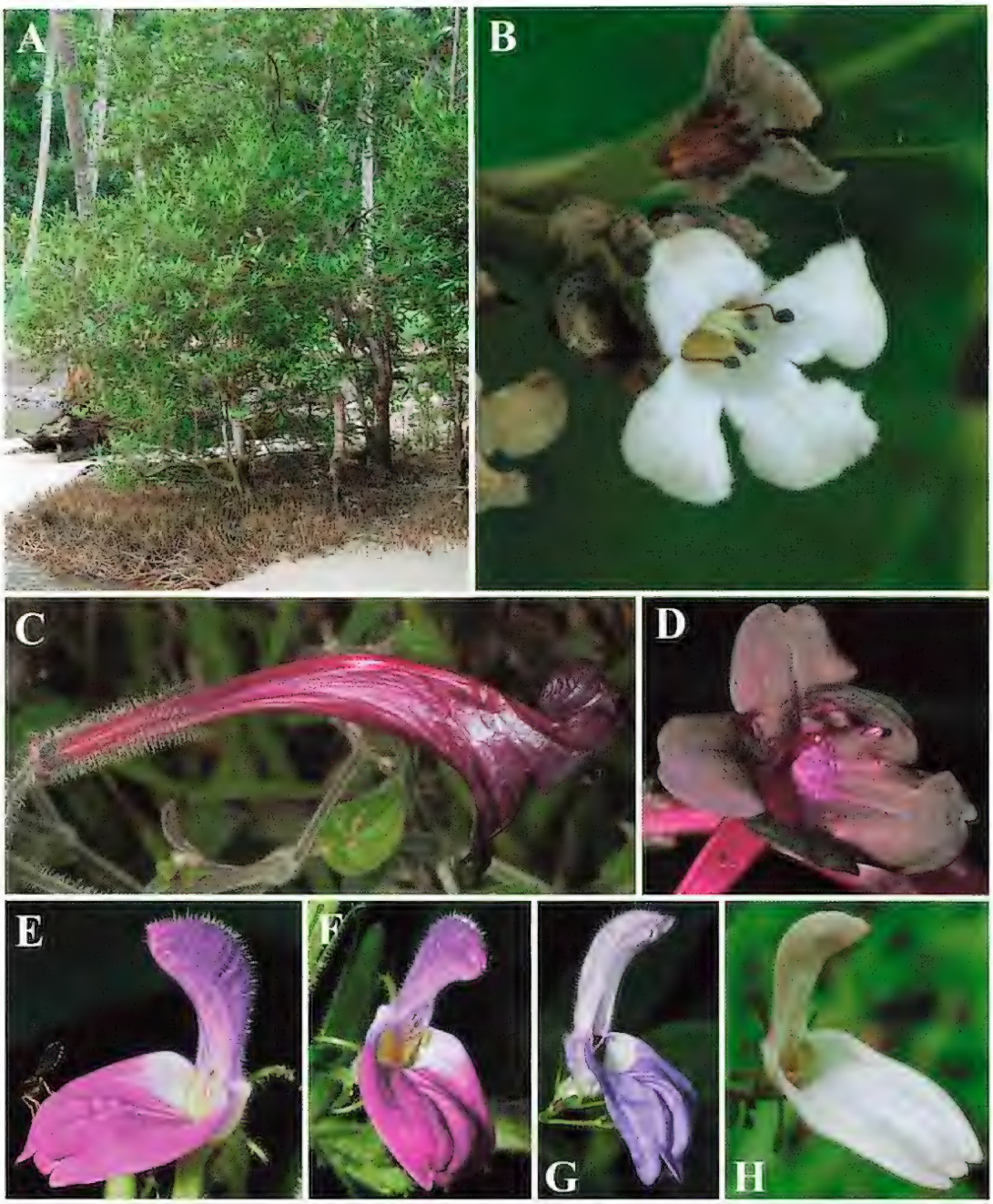

FIGURE 3. Acanthaceae of São Tomé and Príncipe. A. *Avicennia germinans*, habit (*Daniel 11120*). B. *A. germinans*, flower (*Daniel 11120*). C. *Heteradelphia paulowilhelmia*, flower, side view (*Daniel 11139*). D. *H. paulowilhelmia*, flower, view of limb (*Daniel 11139*). E. *Brillantaisia lamium*, flower, side view (*Daniel 11126*). F. *B. lamium*, flower, oblique frontal view (*Daniel 11126*). G. *B. lamium*, flower, color variant (*Daniel 11124*). H. *B. vogeliana*, flower, white form (*Daniel 11113*). Photos by W. Eckerman except A and H by T. Daniel.

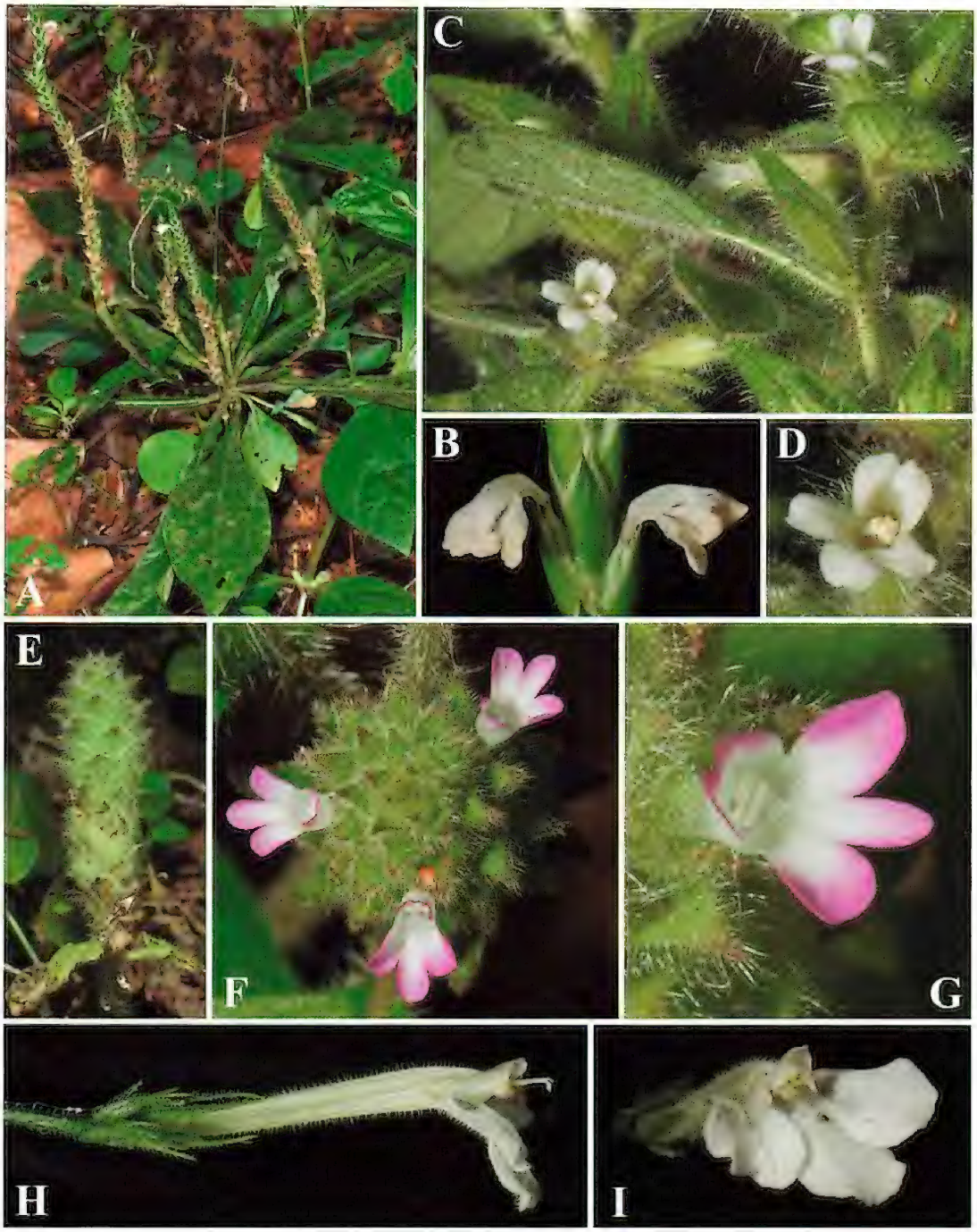

FIGURE 4. Acanthaceae of São Tomé and Príncipe. A. *Elytraria marginata*, habit (*Daniel 11158*). B. *E. marginata*, flowers (*Daniel 11158*). C. *Phaulopsis micrantha*, inflorescences amid leaves (*Daniel 11145*). D. *P. micrantha*, flower (*Daniel 11145*). E. *Nelsonia smithii*, inflorescence, side view (*Daniel 11125*). F. *N. smithii*, inflorescence, top view (*Daniel 11125*). G. *N. smithii*, flower (*Daniel 11125*). H. *Rhinacanthus virens*, flower, side view (*Daniel 11156*). I. *R. virens*, oblique frontal view (*Daniel 11156*). Photos by W. Eckerman.

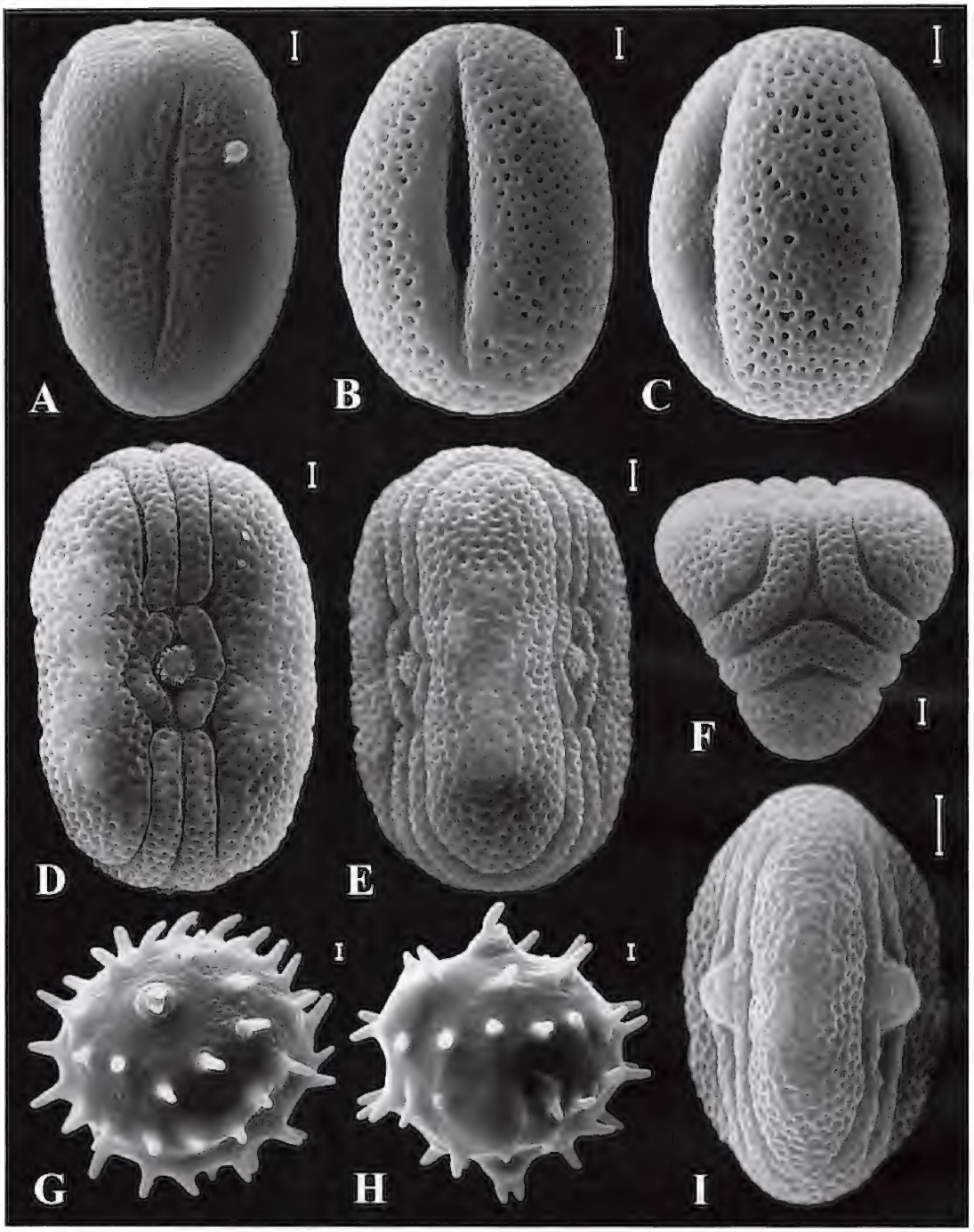

FIGURE 5. SEM images of pollen of Acanthaceae from São Tomé and Príncipe. A. *Acanthus montanus* (*Daniel 11183*), apertural view. B–C. *Avicennia germinans* (*Daniel 11120*), apertural view (B) and interapertural view (C). D–F. *Asystasia gangetica* (*Daniel 11127*), apertural view (D), interapertural view (E), polar view (F). G–H. *Brachystephanus occidentalis* (*Daniel s.n.*), apertural view (G), interapertural view (H). I. *Justicia tenella* (*Daniel 11188*), interapertural view. Scales = 3 μm.

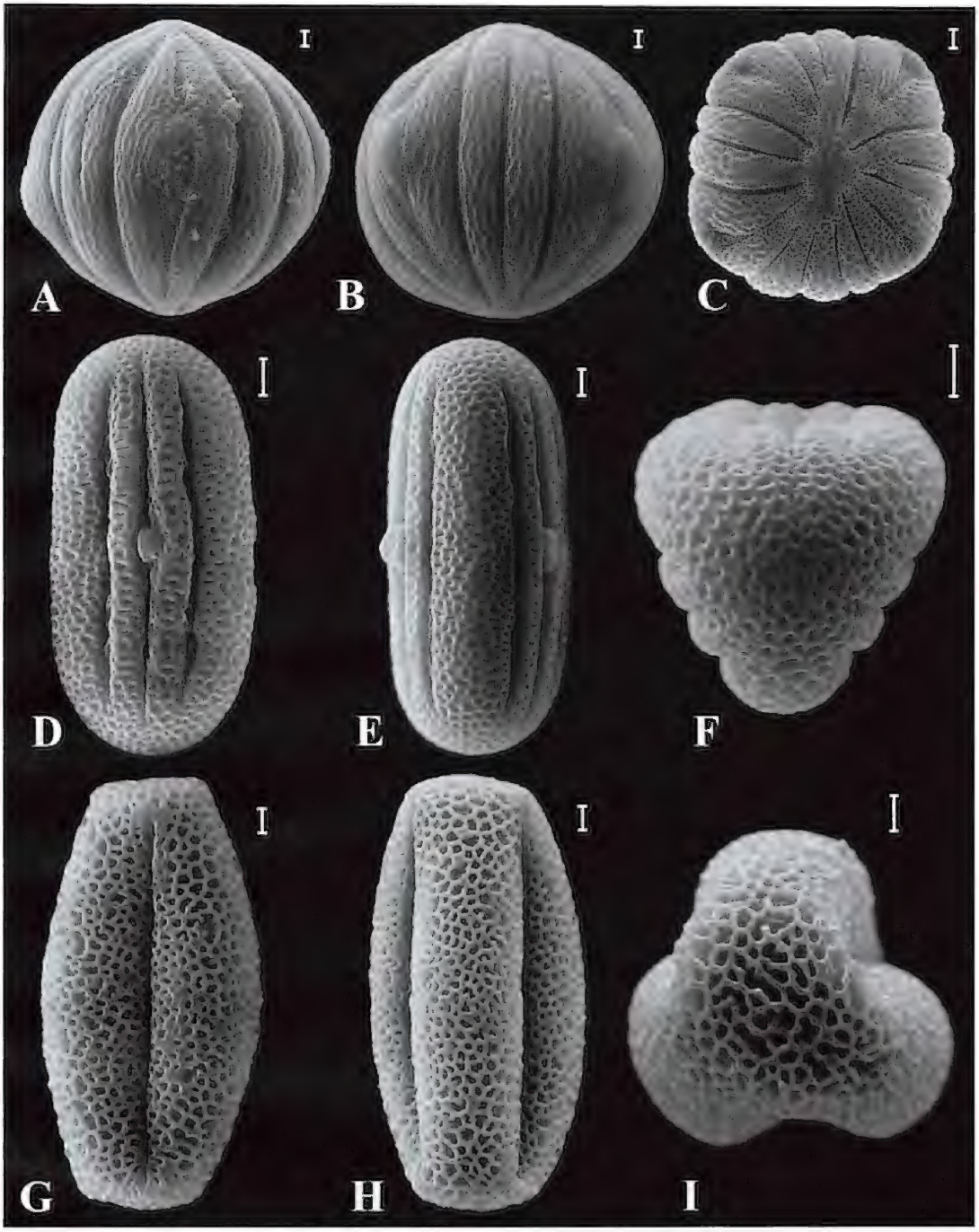

FIGURE 6. SEM images of pollen of Acanthaceae from São Tomé and Príncipe. A–C. *Brillantaisia lamium* (*Daniel 11126*), apertural view (A), interapertural view (B), polar view (C). D–F. *Dicliptera verticillata* (*Daniel 11190*), apertural view (D), interapertural view (E), polar view (F). G–I. *Elytraria marginata* (*Daniel 11158*), apertural view (G), interapertural view (H), polar view (I). Scales = 3 μm.

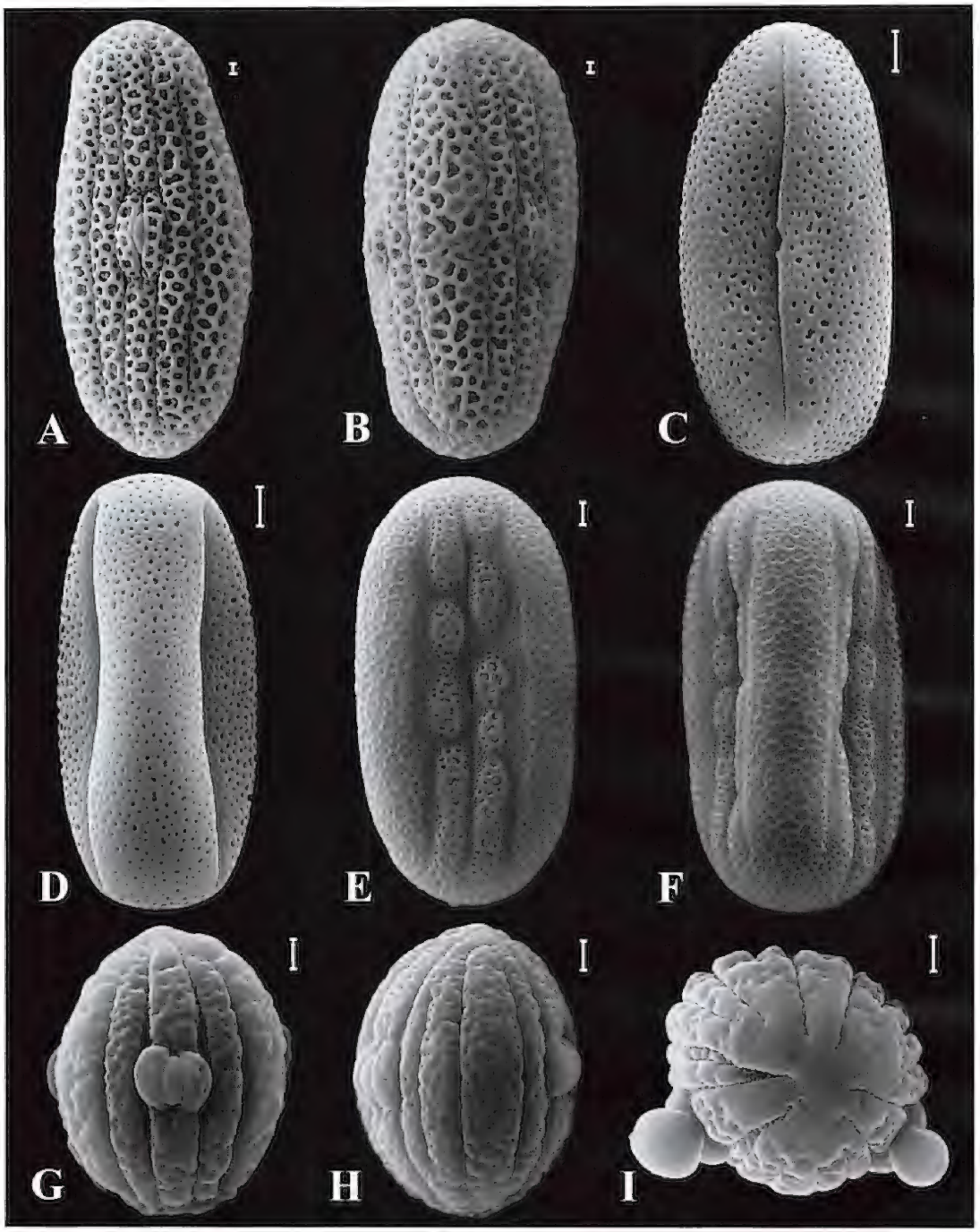

FIGURE 7. SEM images of pollen of Acanthaceae from São Tomé and Príncipe. A–B. *Heteradelphia paulowilhelmia* (*Daniel 11137*), apertural view (A), interapertural view (B). C–D. *Nelsonia smithii* (*Daniel 11186*), apertural view (C), interapertural view (D). E–F. *Rhinacanthus virens* (*Daniel 11156*), apertural view (E), interapertural view (F). G–I. *Phaulopsis micrantha* (*Daniel 11145*), apertural view (G), interapertural view (H), polar view (I). Scales = 3 µm.

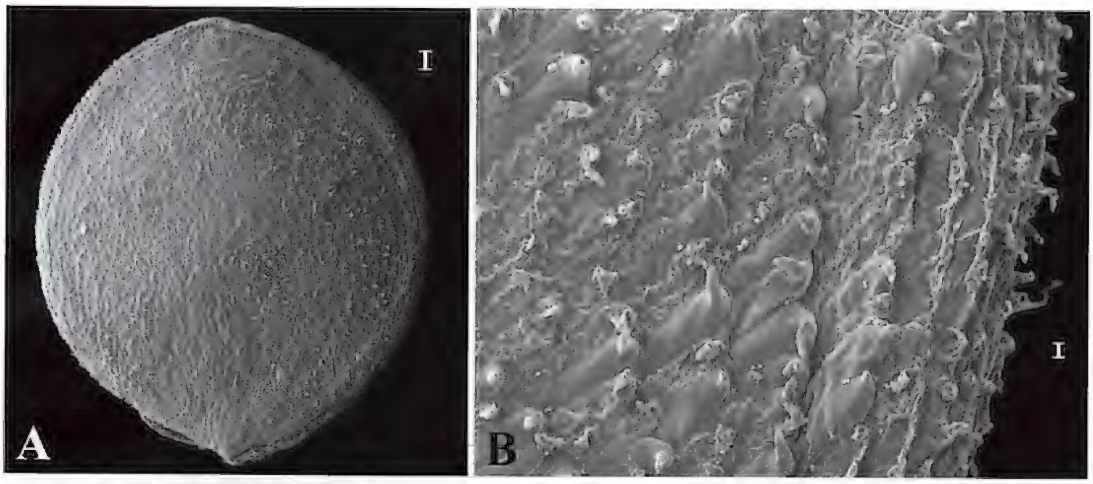

FIGURE 8. SEM image of seed of *Heteradelphia paulowilhelmia* (*Chevalier 13681*). A. Entire seed, scale = 100 μm. B. Magnification of surface and margin, scale = 10 μm.

FIGURE 9. Forms of *Heteradelphia paulowilhelmia*. A. Typical (forest) form on slopes above Lagoa Amélia (photo by W. Eckerman). B. Bog mat form on Lagoa Amélia (photo by R. Drewes).

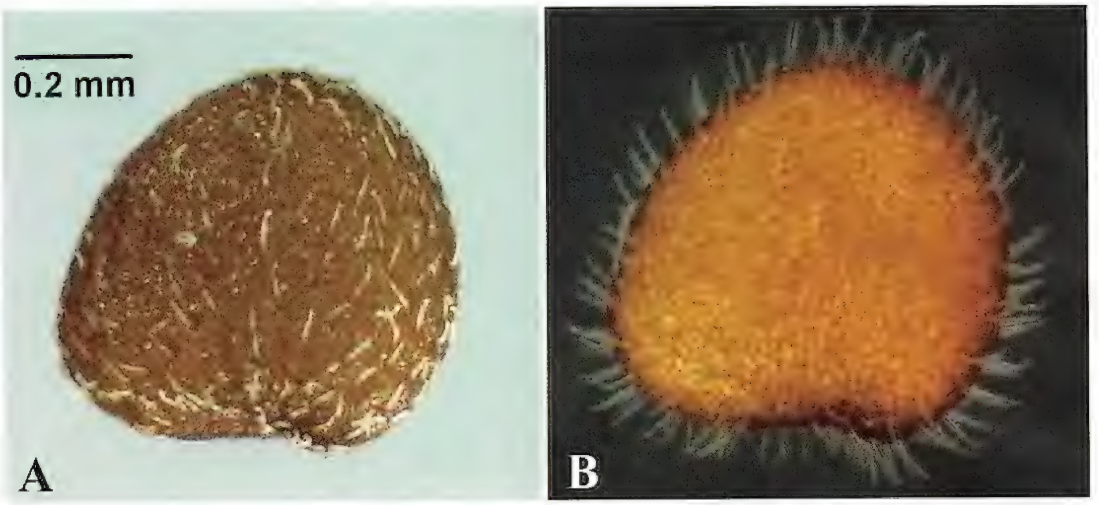

FIGURE 10. Seed of *Justicia tenella* (*Daniel 11188*) with hygroscopic trichomes. A. Fresh, dry seed. B. Same seed when placed in water. Photos by V. Smith.

ADDITIONAL SPECIMENS EXAMINED.— **Príncipe**: without locality, *C. Barter 2036* (K); vicinity of Santa Trindade (= Roça Pico Papagaio) at N slope of Pico Papagaio, between Esperança and São Joaquim (Oeste), 01°37.156′N, 007°23.540′E, *T. Daniel 11157* (CAS, MO, STPH); vicinity of mouth of Rio São Tomé and cove ca. 1 km W on SW coast, 01°33′40.54″N, 007°21′15.51″E, *T. Daniel 11175* (CAS, STPH); SE sector of island, near N base of Os Dois Irmãos, 01°34.889′N, 007°25.548′E to 01°35.728′N, 007°25.263′E, *T. Daniel 11183* (CAS, STPH); Ribeira de Frades, *J. Espírito Santo 228* (COI); between Terreiro Velho and the town [S. António], *A. Exell 540* (COI, K); without locale, *Kealemans s.n.* (L); Roça Sundim [Sundi], *F. Quintas 10* (BR, COI); Praia Rei (Praia Cachochó), ca. 2 km W of plantation Maria Correia, SW corner of island, *J. de Wilde et al. 391* (WAG). **São Tomé**: Belém, *J. Espírito Santo 4795* (COI, LISC); Trindade, 0°17′50″N, 6°41′30″E, *C. de Matos & K. Van Essche 7522* (BRLU, LISC).

Asystasia Blume, Bijdr. 796. 1826

TYPE.— Usually cited as either *Asystasia nemorum* Nees or *A. intrusa* (Forssk.) Bl. (≡ *Ruellia intrusa* Forssk.); however, see discussion by Barker (1986).

Intrusaria Raf., Fl. Tell. 4:66. 1838 ("1836").
Isochoriste Miq., Fl. Ind. Bat. 2:822. 1858.
Dicentranthera T. Anderson, J. Proc. Linn. Soc., Bot. 7:52. 1863.
Parasystasia Baill., Hist. Pl. 10:460. 1891.
Asystasiella Lindau in Engler & Prantl, Nat. Pflanzenfam. 4(3b):326. 1895.
Styasasia S. Moore, J. Linn. Soc., Bot. 37:195. 1905.
Salpinctium T.J. Edwards, S. African J. Bot. 55:7. 1989.

Herbs or subshrubs with cystoliths. Leaves opposite, entire (to irregularly dentate). Inflorescence of unilateral dichasiate spikes or racemes or panicles of spikes or racemes; dichasia usually 1-flowered; bracts and bracteoles small and inconspicuous, the latter sometimes absent. Calyx 5-lobed, lobes equal to subequal in size. Corolla white to yellow to pink to blue to purple, infundibuliform, tube expanded distally into a throat, limb ± 2-labiate, often appearing subactinomorphic with 5 ± equal lobes, lobes ascending-cochlear in bud. Stamens 4, included in or partially exserted from corolla tube; anthers 2-thecous, thecae of a pair equal to subequal in size, parallel to sagittate to subperpendicular, equally to unequally inserted, sometimes with a small basal appendage; pollen 3-colporate, 6-pseudocolpate (pair in mesocolpia sometimes fused into pseudo-

colpal ellipses); staminodes 0. Capsule stipitate, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic). Seeds 2 (or fewer by abortion) per valve, ± discoid, lacking trichomes.

About 40 species occur in tropical regions of the Old World. *Asystasia* pertains to subfamily Acanthoideae, tribe Justicieae, and the "Pseuderanthemum lineage" (McDade et al. 2000).

Asystasia gangetica (L.) T. Anders. in Thwaites, Enum. Pl. Zeyl. 235. 1860. *Justicia gangetica* L., Cent. II. Pl. 3. 1756. **Type.**— "Habitat in India:" LINN Herb. No. 28.27 (lectotype, designated by Malik and Ghafoor in Nasir and Ali, *Fl. Pakistan* 188:68. 1988: LINN).

Asystasia coromandeliana Nees in Wallich, Pl. Asiat. Rarior. 3:89. 1832, nomen superfl.

See Ensermu (1994) for additional synonymy.

Clambering to erect annual to perennial herbs to 6 (–8) dm tall or long, often rooting at nodes; young stems quadrate-sulcate to ± flattened, glabrous or sparsely pubescent with retrorse eglandular trichomes 0.2–0.6 mm long. Leaves petiolate, petioles to 50 mm long (naked portion to 35 mm long), blades ovate to elliptic (to subcordate), 29–100 mm long, 16–44 mm wide, 1.3–2.4 × longer than wide, (acute to) acuminate at apex, (subcordate to) truncate to ± abruptly constricted-attenuate at base (often with a tapering wing along at least distal portion of petiole), margin entire, surfaces sparsely pubescent with eglandular trichomes. Inflorescence of terminal pedunculate unilateral spikes to racemes to 16 cm long (including peduncle), rachis glabrous or pubescent with curved to appressed eglandular trichomes. Bracts triangular to subulate, 1–2 (–2.5) mm long, abaxial surface glabrous or sparsely pubescent with eglandular trichomes. Bracteoles triangular to subulate, 1–1.5 mm long, abaxial surface glabrous or pubescent like bracts. Flowers subsessile to pedicellate, pedicels to 3 mm long. Calyx 5-lobed, 4.5–6.5 mm long (–8 mm long in fruit), lobes linear-lanceolate to lance-subulate, 3–5 mm long, unequal in length (posterior lobe shorter than others), abaxially glabrous or pubescent with antrorse eglandular trichomes or pubescent (especially proximally) with erect glandular trichomes to 0.1 mm long. Corolla white with maroon spots on inner anterior surface of throat and proximal portion of lower lip, (11–) 13–24 mm long, externally pubescent with erect to flexuose to retrorse eglandular trichomes and erect to flexuose glandular trichomes (glandular trichomes sometimes sparse or absent), tube funnelform (i.e., expanded distally into a distinct throat), 9–16 mm long, upper lip deeply 2-lobed, lobes (2–) 4–7 mm long, lower lip deeply 3-lobed, lobes (2–) 4.5–9 mm long. Stamens 4, included in corolla tube, inserted at same height near base of throat, presented at 2 heights, longer pair 5–7 mm long, shorter pair 4–4.8 mm long; thecae 1–2 mm long, subequally inserted, one of a pair offset-angled resulting in the pair appearing asymmetrically subsagittate, at least the lower theca of a pair with a triangular-pointed appendage to 0.2 mm long at base; pollen (fig. 5D–F) 3-syncolporate, endoapertures flanked by 2 curved liplike projections of exine and covered with a spiny membrane, mesocolpia with a pseudocolpal ellipse, interapertural surfaces reticulate. Style slightly exserted from mouth of corolla, 7.5–12 mm long, proximally pubescent with eglandular trichomes; stigma subcapitate, equally 2-lobed. Capsule stipitate, 20–29 mm long, head with a prominent medial constriction (violin shaped), externally pubescent with erect eglandular and glandular trichomes to 0.2 mm long. Seeds 4–4.8 mm long, 3.2–4.1 mm wide, surface warty tuberculate. Figure 2C.

Illustrations.— Heine (1966:137, fig. 27, 1–8); Champluvier (1985:435, fig. 136, 4a–c); Thulin (1993:398, fig. 271); Bosser and Heine (2000:12, pl. 3).

Phenology.— Flowering: December–September; fruiting: February–September.

Distribution and habitats.— Widespread and often weedy in the Paleotropics and naturalized in the Neotropics; distributed throughout most of sub-Saharan Africa (Angola, Benin,

Botswana, Burundi, Cameroon, Central African Republic, Chad, Congo-Brazzaville, Congo-Kinshasa, Equatorial Guinea [Bioko, Río Muni], Ethiopia, Gabon, Gambia, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Malawi, Mali, Mozambique, Namibia, Niger, Nigeria, Rwanda, São Tomé and Príncipe, Senegal, Sierra Leone, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo, Uganda, Zambia, Zimbabwe). It occurs on each of the major islands in the Gulf of Guinea except Annobón. In São Tomé and Príncipe plants occur in disturbed habitats (e.g., cacao plantations, roadsides, trailsides, seashores) in moist to wet lowland to montane forests at elevations from sea level to 320 m.

NOTES.— This widespread species exhibits considerable variation, which has resulted in numerous names attributed to it (see, for example, Clarke 1899b and Ensermu 1994). As represented in São Tomé and Príncipe, *A. gangetica* is variable in size of the corolla and pubescence of both vegetative and reproductive structures. Although appearing primarily as a weed of disturbed habitats in the country, the species was treated by Exell (1973) as native or presumed so. Its putatively native occurrence in parts of the African mainland is similar to that on São Tomé and Príncipe (e.g., Gabon, see Heine 1966). Although it might have been introduced by humans to islands in the Gulf of Guinea, it is treated as native therein. In April of 2008, this species was seen in disturbed regions nearly throughout both islands, especially at elevations less than 500 meters.

Ensermu (1994) recognized two subspecies of *A. gangetica* based primarily on lengths of the corolla and style. Subspecies *micrantha* (Nees) Ensermu has corollas mostly less than 25 mm long and styles mostly less than 15 mm long; it occurs in Africa, Madagascar and other islands in the western Indian Ocean, and the Arabian Peninsula. Plants with usually longer corollas and styles, all occurring from India and Sri Lanka through southeastern Asia and Malesia to Pacific Islands, were referred to the nominate subspecies. Kiew and Vollesen (1997) discussed additional differences between the subspecies and discussed their distributions. All plants from São Tomé and Príncipe conform to subsp. *micrantha*.

ADDITIONAL SPECIMENS EXAMINED.— **Príncipe**: vicinity of Santa Trindade (= Roça Pico Papagaio) at N slope of Pico Papagaio, between Esperança and São Joaquim (Oeste), 01°37.156′N, 007°23.540′E, *T. F. Daniel 11161* (CAS, STPH); Terreiro Velho, *A. Exell 519* (COI, K); Terreiro Velho, 01°40′50″N, 007°27′10″E, *C. de Matos 7734* (LISC); caminho da Fortaleza, *F. Quintas 33* (BR, COI), *s.n.* (LISU); without locality, *F. Welwitsch 5206* (LISU). **São Tomé**: Boa Entrada et environs, *A. Chevalier 13783* (K); along road (EN-1) from São Tomé to Santa Catarina between Conde and Guadalupe, near Água Coimbra (stream), 00°22.917′N, 006°38.889′E, *T. Daniel 11116* (CAS, MO, STPH); along road (EN-2) between São João dos Angolares and Porto Alegre, ca. 56 km S of São Tomé, 00°05.527′N, 006°34.427′E, ca. 5 m, *T. Daniel 11127* (CAS, MO); ca. 3.5–4 km (air) SE of Ponta Figo toward Pico São Tomé, 00°18.642′N, 006°33.398′E, *T. Daniel 11147* (CAS, K, MO, STPH); along road between Santa Catarina and Praia Capito, ca. 2 km S of Sta. Catarina, 00°14.426′N, 006°28.294′E, *T. Daniel 11191* (CAS, STPH); Santa Catarina, *J. Espírito Santo 4650* (LISC); littoral region near the town, *A. Exell 54* (K); Rio Contador, entre o fim do trilho dos túneis, junto ao Tanque, e o túnel no. 8, *E. Figueiredo 207* (LISC); entre Monte Castro (Murvillea) et Ponta Figo, 00°19′N, 006°33′E, *J. Lejoly 95/33* (BRLU); Trindade, 00°17′50″N, 006°41′30″E, *C. de Matos & K. Van Essche 7523* (BRLU, LISC, STPH); Bombaim, *T. Monod 11876* (COI); Io Grande, Rio Io Grande, 00°06′48″N, 006°38′22″E, *R. Odile 109* (BR); São João de Vargem, *F. de Oliveira 233* (STPH); without locality, *Seabra s.n.* (COI); Diana, 00°19′45″N,00 6°41′00″E, *T. Stévart & F. de Oliveira 22* (BRLU); Praia Mikondó, 00°10′00″N, 006°41′00″E, *T. Stévart & F. de Oliveira 66* (BRLU, LISC); Parc National d'Obo, Jachère, Chapelle près de Praia Xuf Xuf, 00°07′45″N, 006°29′45″E, *T. Stévart & F. de Oliveira 159* (BRLU).

Avicennia L., Sp. Pl. 110. 1753.

TYPE.— *Avicennia officinalis* L.

Bontia L. in Loefling, Iter. 193. 1758.
Upata Adanson, Fam. 2:201. 1763.

See Moldenke (1960) and Duke (1991) for a complete list of generic synonyms.

Shrubs or trees lacking cystoliths and with erect aerial roots (pneumatophores) up to 3 dm tall and sometimes with aerial stilt roots. Leaves opposite, entire. Inflorescence of axillary and/or terminal dense (sometimes capitate) pedunculate dichasiate spikes or panicles of spikes; dichasia 1-flowered; flowers subtended by 2 convex bracteoles. Calyx 5-lobed, lobes ± free, convex, imbricate, equal to subequal in size. Corolla white to yellow to orange, actinomorphic to zygomorphic, tube shorter than limb, limb 4(–6)-lobed, lobes ± equal, "imbricate" in bud. Stamens 4 (–6), exserted from mouth of corolla; anthers 2-thecous, thecae of a pair ± equal in size, parallel, equally inserted, lacking basal appendages; pollen 3-colporate (to 3-colpoidate); staminodes 0. Capsule leathery, ± ellipsoid to ovoid (often asymmetric), ± compressed, unilocular, with persistent stylar beak, retinacula absent. Seed 1 (–2) per capsule, consisting mostly of ripe embryo with 2 conspicuous folded cotyledons and a pubescent radicle (cryptoviviparous).

Eight species are recognized along shorelines and tidally influenced waterways in two mostly tropical regions: Atlantic/Caribbean/eastern Pacific (3 spp.) and Indo-western Pacific (5 spp.). *Avicennia* is usually treated either in Verbenaceae or Avicenniaceae. Molecular phylogenetic studies (Schwarzbach and McDade 2002; McDade et al. 2008) reveal it to be nested among Acanthaceae s.l., and either related to *Thunbergia* and *Mendoncia* of subfamily Thunbergioideae or sister to subfamily Acanthoideae. There are eight species of "true" mangroves in western Africa (Corcoran et al. 2007), including *Avicennia germinans* (black mangrove). Although its congeners, *A. mariana* and *A. officinalis* occur in eastern Africa, no other species of *Avicennia* occur in western Africa.

Avicennia germinans (L.) Stearn, Kew Bull. 1958:34. 1958. *Bontia germinans* L., Syst. Nat., ed. 10, 2:1122. 1759. TYPE.— "Habitat in Indiis" [JAMAICA]: *Browne s.n.*, LINN Herb. No. 813.2 (lectotype, designated by Stearn in Kew Bull. 13:35. 1958: LINN). *Avicennia nitida* Jacq., Enum. Pl. Carib. 25. 1760.

Avicennia tomentosa Jacq., Enum. Pl. Carib. 25. 1760.
Avicennia africana P. Beauv., Fl. Oware 1:80. 1806.
Avicennia floridana Raf., Atlantic J. 1:148. 1832.

Shrubs to trees to 10 m tall with pneumatophores under canopy; young stems covered with dense ± antrorsely appressed or matted shiny trichomelike or scalelike projections to 0.05 mm long (scurfy). Leaves petiolate, petioles to 20 mm long, blades narrowly elliptic (to elliptic or obovate), 40–153 mm long, 14–52 mm wide, (1.8–) 2.8–5.9 × longer than wide, acute to rounded at apex, acute to subattenuate at base, margin entire, subrevolute, surfaces minutely punctate, abaxial surface also scurfy. Inflorescence of axillary and terminal pedunculate ± headlike spikes or panicles of these, inflorescence branches (if present) subtended by subovate-concave bracts to 5 mm long, peduncles (5–) 10–50 mm long, scurfy, rachis barely visible, densely pubescent with mostly antrorse eglandular trichomes to 0.2 mm long. Bracts opposite, broadly ovate to subcircular, convex, 2.7–4 mm long, abaxial surface scurfy to pubescent like rachis. Bracteoles similar to bracts. Flowers clustered near apex of peduncles, sessile. Calyx 5-lobed, 3–4 mm long, lobes broadly ovate to subcircular, convex, imbricate, abaxially pubescent with antrorsely appressed eglandular trichomes to 0.4 mm long. Corolla ± leathery, cream to white, 6.5–7.5 mm long, externally

glabrous (tube) and densely pubescent with appressed eglandular trichomes to 0.5 mm long (limb), tube 2.5–3.5 mm long, gradually expanded distally, limb 9–10 mm in diameter, upper lip 2.5–3.5 mm long, apically entire, lower lip 3-lobed, lobes 2.9–4 mm long, inner surfaces of lobes densely pubescent. Stamens 4, exserted from mouth of corolla, inserted at 2 levels near base of tube, longer (posterior) pair 4.3 mm long, shorter (anterior) pair 4 mm long, pairs of thecae presented at 2 heights; thecae gray-purple, 0.7–0.9 mm long; pollen (fig. 5B–C) 3-colpoidate to 3-colporate, colpi and ora verrucate to pilate, interapertural surfaces reticulate. Style exserted from mouth of corolla, 3–3.3 mm long, distally glabrous, proximally pubescent with antrorsely appressed eglandular trichomes; stigma lobes equal, ± spreading, 0.3–0.4 mm long. Fruit subellipsoid, 12–25 mm long, 5–16 mm across at widest expanse, pubescent with antrorsely appressed eglandular trichomes to 0.7 mm long (especially when less mature) and scurfy (especially when more mature). Figure 3A–B.

Illustrations.— Hepper (1963:449, fig. 309); Gibson (1970:178, fig. 32); Correll and Correll (1982:1253, fig. 540); Tomlinson (1986:189, fig. B.8); Villiers (1973:65, pl. 16).

Phenology.— Flowering: January, April, August–October; fruiting: January, April.

Distribution and habitats.— Southern North America (southern USA, Mexico), West Indies, Central America, northern South America, Galapagos Islands, tropical western Africa (Angola, Benin, Cameroon, Congo-Brazzaville, Congo-Kinshasa, Equatorial Guinea [Annobón, Bioko, Río Muni], Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Ivory Coast, Liberia, Mauritania, Nigeria, Senegal, São Tomé and Príncipe, Sierra Leone, Togo); plants occur in marshy ground, tidal flats, mangrove swamps, and foredunes at or near sea level. The species has not been definitively reported from Príncipe, but is known from the other major islands in the Gulf of Guinea: Bioko, São Tomé, and Annobón (Exell 1973). It occurs infrequently along and near protected shores (especially near river mouths) on São Tomé at or near sea level.

Conservation.— Although coastal areas with mangroves have been documented in 11 regions around the island (Corcoran et al. 2007) *Avicennia germinans* is apparently not common on São Tomé. Corcoran et al. (2007) indicate that most mangroves found on islands in the Gulf of Guinea are species of *Rhizophora*, that much of the mangrove forest of São Tomé was destroyed just prior to 1990, and that data on the status of mangroves in São Tomé and Príncipe are scarce. Indeed, they (Cocoran et al. 2007) were unable to confirm the presence of *A. germinans* on São Tomé. Recent collections, noted above, confirm its occurrence on both the northern and southern coasts of the island. Plants do not occur in protected lands, however, and the survival of *A. germinans* on São Tomé is at risk if mangrove communities are destroyed by human activities.

Notes.— As noted by Jarvis (2007), "there has been disagreement over the correct name for this taxon–see Little (in *Phytologia* 8:49–57. 1961) who argued that it should be *A. nitida* Jacq., and Compère (in *Taxon* 12:150. 1963) who favoured *A. germinans* (L.) L." Some authors (e.g., Exell 1944; Moldenke 1960, 1980) have treated African representatives of *A. germinans* as *A. africana* P. Beauv., but most now agree that the latter is conspecific with the former (e.g., Stearn 1958; Gibson 1970; Exell 1973; Tomlinson 1986; Duke 1991).

The black mangrove is often an abundant shrub or tree of tropical shorelines and coastal swamps where it is an important constituent of the mangrove communities. Pneumatophores (aerial, pencil-like structures from horizontal, underground roots that are evident at least at low tide and that are reported to facilitate the uptake of atmospheric oxygen) and cryptoviviparous seeds (that swell, lose their seed coat, and germinate prior to falling) are characteristic of the genus. Flowers of *Avicennia* are often reputed to be an excellent source of honey, and those of plants on São Tomé were observed to be visited by honeybees.

Additional specimens examined.— **São Tomé**: along road (EN-1) from São Tomé to Santa Cata-

rina at Praia das Conchas, 00°24.388′N, 006°37.325′E, *T. Daniel 11120* (BR, CAS, K, MO, STPH); Praia das Conchas, *J. Espírito Santo 4004* (COI), *4133* (LISC); Diogo Nunes, *J. Espírito Santo 4974* (COI, LISC); near Praia dos Tamarindos, *E. Figueiredo & P. Arriegas 93* (K, LISC); alentours de Praia das Conchas, 00°24′25″N, 006°37′35″E, *C. de Matos 7727* (BRLU, LISC); Porto Alegre, Rio Malanza, 00°13′N, 006°44′E, *C. de Matos & K. van Essche 7269* (BRLU, LISC); entre Guadalupe et Praia das Conchas, 00°17′N, 006°37′E, *C. de Matos & K. van Essche 7329* (BRLU, LISC); Rio Malanza, 00°02′07″N, 006°32′05″E, *F. de Oliveira 96* (BRLU).

Brachystephanus Nees in Alph. de Candolle, Prod. 11:511. 1847.

TYPE.— *Brachystephanus lyallii* Nees

Oreacanthus Benth. in Bentham & J.D. Hooker. Gen. Pl. 2:1104. 1876.

Perennial herbs or shrubs with cystoliths. Leaves opposite, entire to crenate. Inflorescence of axillary or terminal dichasiate thyrses, racemes, or spikes (or panicles of these); dichasia 1–6-flowered; flowers usually subtended by 2 bracteoles. Calyx 5-lobed, lobes subequal to unequal in size. Corolla purple, blue, pink, white, or red, tube very short to elongate, cylindric or distally expanded, limb 2-labiate, upper lip entire to 2-lobed, lower lip subentire to 3-lobed, corolla lobes ascending-cochlear in bud. Stamens 2, exserted beyond lips of corolla; anthers 1-thecous, thecae lacking basal appendages; pollen 2–3 (–multi)-porate; staminodes 0. Capsule stipitate, glabrous, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic). Seeds 2 (or fewer by abortion) per valve, discoid, lacking trichomes.

In an unpublished taxonomic account of *Brachystephanus* from 2005 Champluvier (ined.) recognized 24 species that included several undescribed ones and others previously treated in *Oreacanthus*. She also divided the genus into three sections. *Brachystephanus* is restricted to tropical mainland Africa, Madagascar, and islands in the Gulf of Guinea where most species are local endemics that occur in montane habitats. The genus pertains to subfamily Acanthoideae, tribe Justicieae, and subtribe Isoglossinae (Kiel et al. 2006).

Brachystephanus occidentalis Lindau, Bot. Jahrb. Syst. 20:53. 1894. TYPE.— SÃO TOMÉ AND PRÍNCIPE. São Tomé: Monte Café, 850 m, Jun 1888, *F. Quintas 91* (*1300*) (lectotype, designated by Figueiredo & Jury in Kew Bull. 51:761. 1996: K!; isolectotype: COI!).

Perennial herbs or shrubs to 2 m tall; young stems glabrous or pubescent with retrorse to antrorse to erect eglandular trichomes 0.05–0.3 mm long, trichomes ± concentrated in 2 lines. Leaves petiolate, petioles to 41 mm long, blades ovate to elliptic, 25–200 mm long, 8–110 mm wide, 1.8–3.3 × longer than wide, acuminate at apex, rounded to acute at base, adaxial surface glabrous to sparsely pubescent, abaxial surface pubescent (especially along major veins) with eglandular trichomes (and sometimes with some glandular trichomes on smaller, distal leaves). Inflorescence of axillary or terminal dichasiate racemes or thyrses to 70 mm long, rachis puberulent with eglandular and glandular (sometimes inconspicuous or absent) trichomes to 0.05 mm long (puberulent) and sometimes with irregular patches of flexuose to erect multi-septate eglandular trichomes to 0.5 mm long as well; dichasia 1(–many)-flowered (lateral flowers often ± vestigial), sessile to short-pedunculate, peduncles to 1 mm long, puberulent. Bracts triangular to subulate, 1–3 mm long, abaxial surface puberulent. Bracteoles triangular, 0.2–1 mm long, abaxial surface puberulent. Flowers pedicellate, pedicels to 3.5 mm long (accrescent in fruit to 5 mm long). Calyx 3–5.5 mm long, lobes lance-subulate, 2–3.5 mm long, abaxially puberulent. Corolla white with purple tinge on proximal portion of tube to violet, 15–29 mm long, externally puberulent to pubescent with glandular and/or eglandular trichomes to 0.1 mm long (trichomes sometimes inconspicuous), tube ± curved, distally expanded, 11–21 mm long, 2.4–4.2 mm in diameter (measured flat)

at apex, upper lip 4–8 mm long, apically emarginate to 2-lobed, lower lip 2.5–7.5 mm long, apically 3-lobed, lobes 0.2–0.5 mm long. Stamens 12–18 mm long; thecae 1.5–2.3 mm long; pollen (fig. 5G–H) ± spheric, 2-porate, pores smooth to spiny, each surrounded by 2 concentric rings of coarse spines, halves of the grains separated by a discontinuous band of insulae, insulae consisting of irregular gemmae and rugulae. Style 16–29 mm long; stigma subcapitate (2-parted). Capsule 11.5–18 mm long, stipe 5–8 mm long, head 6.5–8 mm long. Seeds 2–2.5 mm long, 1.5–2 mm wide, surface rugose-reticulate. Figure 2D.

Illustrations.— None found.

Phenology.— Flowering: January–September; fruiting: April–August.

Distribution and habitats.— Endemic to the island of São Tomé in São Tomé and Príncipe; plants occur infrequently (especially along streams) in montane primary or secondary forests and in cacao plantations at elevations from 400 to 1630 m.

Conservation.— This narrowly endemic species has a limited distribution, but does not seem particularly rare. Its occurrence at lower altitudes may be threatened by human encroachment and deforestation. Nevertheless, at higher altitudes the species occurs within the protected Parque Natural Obô.

Notes.— *Brachystephanus occidentalis* pertains to sect. *Brachystephanus* (Champluvier, ined). Pollen of *B. occidentalis* is unique in the genus (Figueiredo and Keith-Lucas 1996). Some species of *Brachystephanus* (e.g., *B. africanus* S. Moore) have been noted to be pollinated by sunbirds (Figueiredo & Jury 1996). The color of corollas has been described by collectors as white or violet or pinkish white.

Champluvier and Figueiredo (1996) noted that *Brachystephanus mannii* C.B. Clarke (as *Oreacanthus cristalensis* Champluvier & Figueiredo) had been reported from São Tomé (based on a collection by Mowan in 1913), but that its occurrence there was questionable and yet to be reconfirmed. That species remains definitively known only from Bioko and mainland Africa.

Additional specimens examined.— **São Tomé**: chemin vers Bombaim (00°14.55′N, 006°38.50′E), *G. Joffroy 53* (BRLU, STPH); de Mesa vers Ponta Figo (00°16.75′N 006°33.30′E), *G. Joffroy 176* (BRLU); Rio do Ouro, 00°18.35′N, 006°36.15′E, *G. Joffroy 184* (BRLU, LISC); entre Pico de São Tomé et Monte Castro, 6 km S de Ponta Figo, 00°17′N, 006°33′E, *J. Lejoly 95/12* (BRLU, LISC, STPH); without locality, *G. Mann 1096* (K); entre Pico et Roça Ponta Figo, 00°16′N, 006°33′E, *C. de Matos & K. Van Essche 7390* (BRLU, LISC, STPH); entre Campement du Pico et Morro Vilela, 00°16′N, 006°33′E, *C. de Matos & K. Van Essche 7572* (BRLU, LISC, STPH); Nova Moka, *A. Moller 128* (COI); Monte Café, *A. Moller 281* (COI), *505* (COI), *832* (COI); próx. aos Morros a Monte Café, *A. Moller 327* (COI); sentier W du Pico, *T. Monod 11907* (BM, COI); pente W du Pico, entre Monte Quinas et Quinas Altas, *T. Monod 12005* (BM, COI); Bombaim–Michelangelo (Zona ecológica) (N00°14′03″ E06°39′05″), *F. de Oliveira 489* (BRLU, LISC); near the camp at Morro Vilela (00°17′N, 006°33′E), *F. de Oliveira 1281* (BRLU); Monte Figo, entre a Cascata e Generosa, *J. Paiva 208* (COI); Monte Café, *F. Quintas 1299* (BR); Pico, *Rose* 307 (P); without locality, *Seabra s. n.* (BM, COI); without locality, *F. Welwitsch 5208* (BM, LISU).

Brillantaisia P. Beauv., Fl. Oware 2:67. 1818.

Type.— *Brillantaisia owariensis* P. Beauv.

Belantheria Nees in Alph. de Candolle, Prodr. 11:96. 1847.
Leucorhaphis Nees in Alph. de Candolle, Prodr. 11:97. 1847.
Ruelliola Baill., Bull. Mens. Soc. Linn. Paris 2:852. 1890.

Herbs (annual to perennial) or shrubs with cystoliths; stems square and usually with conspicuously swollen nodes. Leaves opposite, entire to irregularly dentate. Inflorescence usually of terminal dichasiate thyrses, sometimes of axillary dichasia; dichasia (sometimes modified) mostly 3–many-flowered; flowers subtended by 2 bracteoles. Calyx 5-lobed, lobes subequal to unequal in

size, posterior lobe usually larger than others. Corolla white to blue to purple to pink, tube ± cylindric proximally, expanded near apex into an open throat, throat with 2 brownish-yellowish markings internally, limb 2-labiate, upper lip hooded, laterally compressed, apically 2-parted, lower lip apically 3-lobed, corolla lobes left-contorted in bud, 2 membranous pouches evident near junction of base of lower lip and throat of tube. Stamens 2, exserted from tube but usually enclosed in upper lip; anthers 2-thecous, thecae of a pair equal in size, parallel to sagittate, equally inserted, lacking basal appendages; pollen (fig. 6A–C) 4 (–6)-colporate, multi-pseudocolpate; staminodes 0–2, sometimes with vestigial anthers. Capsule estipitate, linear-ellipsoid, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic). Seeds 6–30 (or fewer by abortion) per valve, discoid to reniform, covered with hygroscopic trichomes.

Thirteen species are known from tropical Africa and Madagascar, with a center of distribution in the Guineo-Congolian rain forests; several species are cultivated. The genus pertains to subfamily Acanthoideae, tribe Ruellieae. Three species occur in São Tomé and Príncipe.

1. Capsule glabrous (or with a few eglandular trichomes at apex), 23–31 mm long; leaves entire (to subcrenate) ..... *B. lamium*
1. Capsule pubescent throughout with eglandular and glandular trichomes, 12–21 mm long; leaves crenate to dentate.
   2. Weak herbs to 6 dm tall; corolla 17–23 mm long, whitish or purplish; internodes pubescent; petioles winged distally, with a naked portion proximally ..... *B. vogeliana*
   2. Stout herbs or shrubs to 4.5 m tall; corolla ca. 54 mm long, purplish; internodes glabrous; petioles winged to node (lacking a naked portion) ..... *B. owariensis*

Brillantaisia lamium (Nees) Benth. in W. Hooker, Niger Fl. 477. 1849. *Leucorhaphis lamium* Nees in Alph. de Candolle, Prodr. 11:97. 1847. **Type**.— NIGERIA. "ad Cap Palmas in Guineâ superiori, locis apertis" [fide protologue], *Ansell s.n.* (syntype: K ex herb. Benth.); "ibidem in littore arenoso," November, *Vogel s.n.* (syntype: K ex herb. Hook.).

Brillantaisia palisotii Lindau, Bot. Jahrb. Syst. Pflanz. 17:99. 1893. **Type**.— SIERRA LEONE. "Kort-Right-Hill bei Freetown," 12 Feb 1886, *Preuss 16* (?); Freetown, *Afzelius s.n.* (UPS); TOGO. "Ketschenkebach bei Bismarcksburg," 26 Sep 1890, *Büttner 231* (?), 5 Nov 1890, *Büttner 320* (?); CAMEROON. "Mungo," Sep 1874, *Buchholz s.n.* (BM); SÃO TOMÉ AND PRÍNCIPE. São Tomé: Saudade, Dec 1887, *F. Quintas 1132* (= *89*) (COI!); São Tomé: Roça Rio do Ouro, Mar 1888, *F. Quintas 1235* (= *88*) (BM, BR!, COI!, Z); "Baschilangegebiet: am Lulua," *Pogge 1123* (?). Most or all of the syntypes were presumably at B, where Lindau worked. Specimens cited above are either syntypes or isosyntypes.

Brillantaisia eminii Lindau, Bot. Jahrb. Syst. 17:103. 1893.

Brillantaisia subcordata De Wild. & T. Durand, Bull. Soc. Roy. Bot. Belgique 38:44. 1899.

Brillantaisia subcordata var. *macrophylla* De Wild. & T. Durand, Contrib. Fl. Congo 1, 2:47. 1900.

Decumbent to erect annual herbs to 8 (–10) dm tall, sometimes rooting at nodes; young stems quadrate-sulcate, nearly glabrous to pubescent on angles to ± evenly pubescent with flexuose multi-septate eglandular and glandular trichomes 0.3–2.5 mm long (nodes with coarser trichomes to 4 mm long). Leaves petiolate or distalmost pair becoming subsessile, petioles (naked portion) to 105 mm long, blades broadly ovate to ovate, 19–135 mm long, 14–97 mm wide, 1–1.9 × longer than wide, acuminate at apex, acute- to rounded- to truncate-attenuate at base with laminar tissue tapering (forming a narrow wing) along distal portion of petiole, margin entire (rarely subcrenate), surfaces pubescent on veins and intercostals regions with coarse and flexuose eglandular trichomes. Inflorescence of terminal dichasiate thyrses, rachis proximally glabrous or pubescent with flexuose eglandular trichomes or pubescent with eglandular and glandular trichomes, distally ±

evenly pubescent with flexuose multi-septate glandular trichomes 0.5–1.5 mm long (glandular pubescent); dichasia pedunculate, peduncles 13–33 mm long, secondary peduncles (if present) to 17 mm long. Bracts subfoliose (reduced in size distally), distal bracts subsessile, ovate to elliptic to obovate, 4.3–9.5 mm long, 1.4–6.5 mm wide. Bracteoles linear to oblanceolate, 1–2.5 mm long, 0.3–0.5 mm wide, secondary bracteoles (if present) similar to bracteoles except smaller. Flowers pedicellate, pedicels 1–4 mm long. Calyx 5.2–8 mm long (up to 10 mm long in fruit), lobes subequal, linear to lanceolate, abaxially glabrous to sparsely glandular pubescent, margin glandular pubescent. Corolla blue to violet with white at base of lower lip and with paired blackish swellings in mouth, 25–35 mm long, externally glandular pubescent, tube 10–12 mm long, narrow proximal portion 5–7 mm long, upper lip 17–22 mm long, lower lip 20–25 mm long. Anther thecae 3.5–5.2 mm long, pubescent; staminodes 2, 3 mm long. Capsule 23–31 mm long, glabrous or pubescent only at apex with a few eglandular trichomes to 0.5 mm long; ovules 18 per valve. Seeds 2 mm long, 1.5 mm wide, covered with appressed hygroscopic trichomes to 0.5 mm long when wet. Figure 3E–G.

Illustrations.— Heine (1963:406, fig. 300); Heine (1966:87, fig. 17, 4–8); Sidwell (1998:98, fig. 14).

Phenology.— Flowering and fruiting: all year.

Distribution and habitats.— Tropical Africa (Angola, Burundi, Cameroon, Central African Republic, Congo-Kinshasa, Equatorial Guinea [Bioko], Ethiopia, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Nigeria, São Tomé and Príncipe, Sierra Leone, Sudan, Tanzania, Togo, Uganda); plants occur in regions of wet forest, but often in disturbed areas therein. In São Tomé and Príncipe plants occur in moist to wet lowland and montane forests, primarily in disturbed habitats (roadbanks, cacao plantations, along streams), at elevations from 5 to 1230 m.

Local names.— "Fiá fôgô" (*Espírito Santo 4727*); "fiá-de-mina-grande" (*Lains & Silva 18*).

Notes.— Corollas are rarely described as white (e.g., *Moller 301*) or as purple (e.g., *Moller 297*). Considerable variation in leaf size among populations was encountered: *Daniel 11114* consists of plants with small leaves (blades 19–44 mm long) whereas *Daniel 11124* consists of plants with larger leaves (blades 57–115 mm long). *Daniel 11184* is a mixed population of both *B. lamium* (*11184a*) with entire leaves and nearly glabrous capsules and purple-flowered *B. vogeliana* (*11184b*) with crenate-dentate leaves and densely pubescent capsules. These species thus occur sympatrically and hybrids between them should be sought. Indeed, rare individuals of *B. lamium* with subcrenate leaf margins might result from interaction between these species.

Additional specimens examined.— **Príncipe**: vicinity of Santa Trindade (= Roça Pico Papagaio) at N slope of Pico Papagaio, between Esperança and São Joaquim (Oeste), 01°37.156′N, 007°23.540′E, *T. Daniel 11160* (CAS, MO); 1–2 km SW of aeroporto on road toward Pico Papagaio, 01°38.296′N, 007°23.877′E, *T. Daniel 11162* (CAS); Terreiro Velho, plantation, *A. Exell 533* (COI, K); without locale, *G. Mann 1142* (K); Paciência, 01°40′30″N, 007°26′10″E, *C. de Matos 7737* (LISC); without locality, *J. de Souza s.n.* (LISU); without locality, *F. Welwitsch 5205* (LISU). **São Tomé**: RDSTP Parque Nacional Ôbó, Ponte Canê [00°07′N, 006°34′E], *S. Carvalho 24* (BRLU, LISC); vicinity of Macambrará Radio Tower above Bom Sucesso, 00°16.560′N, 006°36.324′E, *T. Daniel 11114* (CAS, K, MO, STPH); along road (EN-2) between Ribeira Afonso and São João dos Angolares, ca. 38 km S of São Tomé, 00°08.511′N, 006°39.558′E, *T. Daniel 11124* (CAS, K, MO, STPH); along road (EN-2) between São João dos Angolares and Porto Alegre, ca. 56 km S of São Tomé, 00°05.527′N, 006°34.427′E, *T. Daniel 11126* (CAS, STPH); along road from Trindade to Bombaim, 6.2 km SW of jct. São Tomé-Bom Sucesso road, 00°16.560′N, 006°38.816′E, *T. Daniel 11184* (CAS, K, MO, STPH); along road between Santa Catarina and Praia Capito, ca. 3.5 km S of Sta. Catarina, 00°13.903′N, 006°28.539′E, *T. Daniel 11193* (CAS, STPH); along road between Santa Catarina and Praia Capito, ca. 3.5 km S of Sta. Catarina, 00°13.903′N, 006°28.539′E, *T. Daniel 11195* (CAS, STPH, US); Famosa, *J. Espírito Santo 67* (COI, NCU); Ribeira Peixe, Dependência Vila José–Caminho de Vila

Verde, *J. Espírito Santo 3870* (COI, LISC); Água d'Agô, *J. Espírito Santo 4312* (LISC), *4313* (LISC); S. Miguel, *J. Espírito Santo 4727* (COI, LISC); Ilhéu das Rôlas, *J. Espírito Santo 5118* (COI, LISC); between Monte Café and Nova Moca, *E. Figueiredo & P. Arriegas 31* (LISC); Caue, Prop Rio Ió Grande, *N. Gabaldá 9/Ne* (COI); chemin des Pico Formoso (00°14.80′N 6°38.00′E), *G. Joffroy 43* (BRLU); Água de Dilas [Velas], 00°15′N, 006°37′E, *J. Lejoly 93/602* (BRLU); San Miguel (près de l'eglise et de la garrison), 00°08′N, 006°30′E, *J. Lejoly 95/119* (BRLU, LISC); de Bom Sucesso vers Macambrará, *J. Lejoly 97/299* (BRLU, LISC, STPH); Monte Café, *Lains & Silva 18* (LISU); Roça Saudade, *A. Moller 74* (COI); Roça Nova Moka, *A. Moller 131* (COI); Blu-Blu, *A. Moller 297* (COI), *301* (COI); Mongo (Monte Café), *A. Moller 576* (COI); au-dessus de Monte Café, *T. Monod 11686* (COI); Vale Carmo, *M. Ogonovszky 34* (BRLU); Bacia da Ribeira Anna Ambó, *F. Quintas 1404* (COI); without locale, *Sebra s.n.* (COI); Saudade, waterfall, *G. Watt 7049* (MO).

Brillantaisia owariensis P. Beauv., Flore d'Oware 2:68. 1818. **Type.**— "Nigeria, Benin, Agathon" (fide Sidwell 1998), *Palisot de Beauvois s.n.*" (lectotype, fide Sidwell (1998): G; isolectotypes: G).

Belantheria belvisiana Nees in Alph. de Candolle, Prodr. 11:96. 1847.
Brillantaisia patula T. Anders., J. Proc. Linn. Soc., Bot. 7:21. 1864.
Brillantaisia alata T. Anders. ex Oliv., Trans. Linn. Soc. London 29:125. 1875.
Brillantaisia salviiflora Lindau, Bot. Jahrb. Syst. 17:101. 1893.
Brillantaisia nitens Lindau, Bot. Jahrb. Syst. 17:102. 1893.
Brillantaisia dewevrei De Wild. & Th. Dur., Bull. Soc. Roy. Bot. Belgique 38:44. 1899.
Brillantaisia nyanzarum Burkill, Fl. Trop. Afr. 5:39. 1899.
Brillantaisia leonensis Burkill, Fl. Trop. Afr. 5:41. 1899.
Brillantaisia patula var. *welwitschii* Burkill, Fl. Trop. Afr. 5:41. 1899.
Brillantaisia mahonii C.B. Clarke, Bull. Misc. Inform. 1906:251. 1906.
Brillantaisia bauchiensis Hutch. & Dalziel, Fl. W. Trop. Afr. 2:253. 1931.

Erect herbs to 3.5 m tall; young stems quadrate-sulcate, internodes glabrous, nodes pubescent with coarse and straight to flexuose eglandular trichomes to 1.8 mm long. Leaves petiolate, petioles winged to node (i.e., lacking naked portion), to 140 mm long, blades (excluding wing of petiole) ovate to broadly ovate, 75–280 mm long, 57–170 mm wide, 1.3–2.3 × longer than wide, acuminate to short-acuminate at apex, acute- to rounded- to truncate-attenuate at base with laminar tissue tapering along petiole to node, margin irregularly coarsely crenate-dentate (wing of petiole entire or becoming entire proximally), surfaces sparsely pubescent (primarily along veins) with flexuose to curved eglandular trichomes to 0.4 mm long. Inflorescence of terminal dichasiate thyrses, rachis puberulent with an understory of erect trichomes to 0.05 mm long and sometimes with an overstory of erect to flexuose eglandular trichomes to 0.2 mm long; dichasia pedunculate, peduncles to 35 mm long, secondary peduncles (if present) to 20 mm long. Bracts often caducous, subfoliose, ± petiolate, 17–35 mm long, 7–15 mm wide. Bracteoles subfoliose, often caducous, obovate to elliptic, 10–11 mm long, 4–5.5 mm wide, secondary bracteoles similar to bracteoles except smaller. Flowers pedicellate, pedicels to 3 mm long. Calyx 21.5 mm long, lobes subequal to unequal (one longer than others), oblanceolate to spatulate, widest near apex, abaxially and marginally pubescent with erect to flexuose eglandular and glandular trichomes 0.05–0.3 mm long. Corolla blue, 54 mm long, externally pubescent with erect to flexuose glandular trichomes to 1.5 mm long, tube 21 mm long, narrow proximal portion 11 mm long, upper lip 30 mm long, lower lip 34 mm long. Androecium not seen. Capsules not seen, reported by Sidwell (1998) as pubescent with eglandular and glandular trichomes.

Illustrations.— Oliver (1875: t. 124); Heine (1966:93, fig. 19, 1–6, as *B. patula*); Champluvier (1985:447, fig. 139, 2–3).

Phenology.— Flowering: plants collected in April from a large population (*Daniel 11194*)

were all sterile, as were plants collected by Figueiredo in August. *Moller 90* is a flowering collection from 1885 but without month of collection indicated.

Distribution and habitats.— Throughout tropical Africa (Angola, Burundi, Cameroon, Central African Republic, Congo-Brazzaville, Congo-Kinshasa, Gabon, Ivory Coast, Kenya, Liberia, Nigeria, Rwanda, São Tomé and Príncipe, Sierra Leone, Sudan, Tanzania, Togo, Uganda); also naturalized in various tropical regions elsewhere (e.g., La Réunion [Bosser & Heine 2000]); plants generally occur in moist montane forest and recently disturbed areas at 600–1600 m. In São Tomé and Príncipe plants occur in secondary forests and in disturbed habitats (e.g., cacao plantations, roadsides) in regions of lowland moist to wet forests at elevations near 100 m only on São Tomé.

Conservation.— Although the species is widely distributed in tropical Africa, based on the number of known collections, it appears to be rare in São Tomé. Because it seems to be restricted to disturbed habitats there, it might be more common on the island than suggested by collections.

Local name.— "Mamblembê" (Figueiredo 2002).

Ethnobotany.— Decoctions of leaves of an unidentified species of *Brillantaisia* (local name: "mamlêblê") from São Tomé are used to treat measles and small wounds (Sequeira 1994).

Notes.— This species was treated by Sidwell (1998) and Vollesen (2008) as the most widespread and variable in the genus. Various distinctive forms are sometimes evident in some regions of Africa. Names that have been applied to plants from islands in the Gulf of Guinea include *B. patula* and *B. nitens* (Exell 1973). Because there are few collections of this species from São Tomé and Príncipe, and most of those lack flowers and fruits, the description above is only partially complete. Sidwell (1998) provided a complete description of the species from throughout its range. Plants referable to *B. owariensis* on São Tomé pertain to the "*patula* group" (i.e., open and lax inflorescence, large flowers, and petiole winged to the node) as discussed by Sidwell (1998). Exell (1944) cited an additional collection from São Tomé (*Chevalier 14368*, from Boa Entrada) that was not seen by us.

Additional specimens examined.— **São Tomé:** along road between Santa Catarina and Praia Capito, ca. 3.5 km S of Sta. Catarina, 00°13.903′N, 006°28.539′E, *T. F. Daniel 11194* (CAS); Blublu, *E. Figueiredo 213* (LISC); without locality, *A. Moller 90* (COI).

Brillantaisia vogeliana (Nees) Benth. in W. Hooker, Niger Fl., 477. 1849. *Leucorhaphis vogeliana* Nees in Alph. de Candolle, Prodr. 11:97. 1847. **Type.**— EQUATORIAL GUINEA. Bioko ["Fernando Po"]: without locality, November, *Vogel 179* ["145" fide protologue] (holotype: K ex herb. Hook.; isotypes: K).

Brillantaisia molleri Lindau, Bot. Jahrb. Syst. 17:99. 1893. **Type.**— SÃO TOMÉ AND PRÍNCIPE. São Tomé: prox. á Cachoeira do Manuel Jorge (Roça São Nicolau) [fide specimen at COI], May 1885, *A. Moller 87* [= 33; based on specimen at COI] (lectotype, designated here: COI!; isolectotype: K!).
Brillantaisia preussii Lindau, Bot. Jahrb. Syst. 17:100. 1893.
Brillantaisia soyauxii Lindau, Bot. Jahrb. Syst. 17:101. 1893.
Brillantaisia schumanniana Lindau, Bot. Jahrb. Syst. 17:102. 1893.

Erect herbs to 6 dm tall, sometimes rooting at nodes; young stems quadrate-sulcate, internodes ± 2-fariously pubescent with conspicuous multi-septate ± appressed eglandular trichomes to 0.5 mm long, nodes with similar but spreading trichomes up to 2 mm long. Leaves petiolate or becoming subsessile distally, petioles (naked portion) to 85 mm long, blades broadly ovate to ovate to elliptic, 24–195 mm long, 17–118 mm wide, 0.9–2.3 × longer than wide, acute to acuminate at apex, acute- to rounded- to truncate-attenuate at base with laminar tissue tapering along distal portion of petiole, margin crenate-sinuate to coarsely and irregularly dentate, adaxial surface pubes-

cent (especially along midvein, sparse elsewhere) with coarse cauline type trichomes, abaxial surface sparsely puberulent (especially along midvein) with eglandular and sometimes glandular trichomes. Inflorescence of terminal ± leafy dichasiate thyrses, rachis evenly pubescent with an understory of erect to flexuose eglandular and glandular trichomes 0.1–0.3 mm long and an overstory of erect to flexuose glandular trichomes to 1 mm long and sometimes also with flexuose eglandular trichomes (at least proximally) to 2 mm long; dichasia pedunculate, peduncles 6–14 mm long, secondary peduncles to 12 mm long. Bracts foliose or reduced in size distally, distal bracts ± petiolate, ovate to elliptic to obovate, 5–15 mm long, 2–6 mm wide. Bracteoles elliptic to obovate, 3.5–8 mm long, 0.6–2.5 mm wide, secondary bracteoles similar to bracteoles or smaller. Flowers pedicellate, pedicels 2–3 (–5) mm long. Calyx 7–10 mm long (up to 16 mm long in fruit), lobes unequal, spatulate, abaxially pubescent like rachis (or with the trichomes mostly glandular), margin sometimes ciliate with flexuose eglandular trichomes to 2 mm long. Corolla (see floral notes below) white (sometimes with faint purple veins on lower lip and drying purplish) or purplish with a white area at base of lower lip, 17–23 mm long, externally pubescent with flexuose subglandular to glandular trichomes to 0.5 mm long, tube 6–8 mm long, narrow proximal portion 4–6 mm long, upper lip 11–16 mm long, lower lip 10–17 mm long. Anther thecae 2–3.7 mm long, pubescent; staminodes 2, 5–7 mm long. Capsule 12–21 mm long, pubescent with erect glandular and eglandular trichomes 0.05–0.3 mm long; ovules 16–30 per valve. Seeds 1–1.3 mm long, 0.7–1.2 mm wide, covered with appressed (± invisible) hygroscopic trichomes to 0.5 mm long when wet. Figure 3H.

Illustrations.— Heine (1966:91, fig. 18, 1–6); Sidwell (1998:96, fig. 13).

Phenology.— Flowering and fruiting: January–October.

Distribution and habitats.— Tropical Africa (Cameroon, Central African Republic, Congo-Kinshasa, Equatorial Guinea [Bioko], Gabon, Ghana, Ivory Coast, Kenya, Nigeria, São Tomé and Príncipe, Sudan, Uganda); plants occur, often as a weed, in disturbed habitats (e.g., waste ground, clearings, along trails and roads, and in plantations). In São Tomé and Príncipe plants occur only on São Tomé in moist to wet primary and secondary forests and in disturbed habitats (roadsides, trailsides) at 300 to 1350 m.

Notes.— The holotype of *Brillantaisia molleri* at B was destroyed; a lectotype for this name is designated above based on the isotypes at COI and K. Based on differences seen among Daniel's 2009 collections of this species, the white-flowered plants have leaves with a generally more truncate (vs. more rounded to attenuate) base and capsules with fewer (16–20 vs. ca. 30) ovules per capsule valve than purple-flowered plants. Exell (1944:261) noted that the two forms appeared to be identical (except for the flower color) "and always grow together, the purple-flowered form being rather more common." Plants observed by Daniel during April of 2009 in São Tomé did not occur in populations with both blue and white corollas; rather, either blue-flowered or white-flowered populations were encountered. White flowers sometimes had bluish veins on the lower lip of the corolla and appear generally bluish on drying.

In corollas of this species, the lower lip forms a saccate pouch near and at its junction with the corolla tube. On the posterior side of this pouch, there is a brownish-translucent window at the mouth of the corolla in the middle of which there is a trough (presumably providing access to nectar at the base of the tube). The upper lip is conduplicate (enclosing the stamens and style) and closed for between ⅛ and ½ its length in the mid-portion where the edges are connivent. The stigma is purple and sometimes emerges (with the longer lobe recurved downward and the shorter lobe held straight or erect) from the upper lip distal to the "closed" portion. The stigma is presented either proximal to or at the same level as the anthers. The flowers are nototribic with the anthers opening toward the lower lip.

Additional specimens examined.— **São Tomé**: Pico, *Campos 17* (COI); vicinity of Macambrará Radio Tower above Bom Sucesso, 00°16.560′N, 006°36.324′E, *T. Daniel 11113* (BR, CAS, K, MO, STPH, US); trail from Jardim Botânico de Bom Sucesso (00°16.866′N, 006°38.868′E, 1115 m) to Lagoa Amélia (00°15.972′N, 006°35.589′E, 1480 m), along lower reaches of trail, *T. Daniel 11129* (CAS, K), *11131* (CAS, MO); Famosa, *J. Espírito Santo 68* (COI, NCU); Quinta da Graça, *J. Espírito Santo 128* (COI); Monte Café, *J. Espírito Santo 4298* (LISC), Vanhulst (Macambrará), *A. Exell 88* (COI, K), *100* (COI, K); between Monte Café, and Nova Moca, *E. Figueiredo & P. Arriegas 32* (K, LISC); road from Nova Moca to the waterfall of Manuel Jorge River (Cascata), *E. Figueiredo & P. Arriegas 33* (K, LISC); near São Nicolau, road from São Nicolau to Macambrará, *E. Figueiredo & P. Arriegas 66* (K); Lemba, Prop Dependência Manuel Morais, *N. Gabaldá 44/Ne* (COI); chemin vers Bombaim , 00°14.55′N, 6°38.50′E, *G. Joffroy 50* (BRLU); chemin de Lagoa Amélia, 00°17.25′N, 006°36.40′E, *G. Joffroy 77* (BRLU); Água das Dilas [Velas] vers Lagoa Amélia, 00°16′N, 006°36′E, *J. Lejoly 93/610* (BRLU), *93/611* (BRLU); entre Pico de São Tomé et Monte Castro, 6 km S de Ponta Figo, 00°17′N, 006°33′E, *J. Lejoly 95/22* (BRLU, STPH); entre Pico de São Tomé et Monte Castro, 6 km S de Ponta Figo, 00°17′N, 006°33′E, *J. Lejoly 95/28* (BRLU, LISC, STPH); entre Calvário et Lagoa Amélia, 00°16′N, 006°35′E, *J. Lejoly 95/79* (BRLU, LISC, STPH); vic. Bom Sucesso, 00°17′N, 006°37′E, *J. Lejoly 95/82* (BRLU, LISC, STPH); Bom Sucesso vers Lagoa Amélia (sentier S.1, km 0 a 0.14), *J. Lejoly 97/211* (BRLU, LISC); entre Macambrará et Zampalma, *J. Lejoly 97/326* (BRLU, LISC, STPH); entre Bom Sucesso et Lagoa Amélia, 00°17′N, 006°37′E, *C. de Matos & K. van Essche 7294* (BRLU, LISC, STPH); Bom Sucesso, 00°17′N, 006°37′E, *C. de Matos & K. van Essche 7421* (BRLU, LISC, STPH); Macambrará-Zampalma, 00°16′02″N, 06°37′08″E, *C. de Matos 7471* (BRLU, LISC); Bom Sucesso, chemin Lagoa Amélia, 00°17′30″N, 06°36′45″E), *T. Stévart & F. de Oliveira 56* (BRLU, LISC), *57* (LISC); Roça Saudade, *A. Moller 45* (COI); Monte Café, *A. Moller 607* (COI); entre S. Pedro et Lagoa Amélia, *T. Monod 11718* (COI); Calvário, *T. Monod 11857* (COI); Parc Nat. d'Obo, Bom Sucesso, chemin Lagoa Amélia, 00°17′30″N, 006°36′45″E, *T. Stévart & F. de Oliveira 56* (LISC, STPH), *57* (BRLU, LISC, STPH); Cascata (00°18′00″N, 06°33′30″E), *T. Stévart & F. de Oliveira 143* (BRLU); São Nicolau, *J. de Wilde et al. 3* (WAG); road crossing from S. João dos Angolares to Ribeira Peixe with the Rio Grande, near bridge, *J. de Wilde et al. 95* (WAG).

Dicliptera Juss., Ann. Mus. Natl. Hist. Nat. 9:267. 1807, nom. cons.

Type.— *Dicliptera chinensis* (L.) Juss. (≡ *Justicia chinensis* L.).

Diapedium K.D. Koenig, Ann. Bot. (König & Sims) 2:189. 1805, nom. rej.
Solenochasma Fenzl in J. Jacquin, Eclog. Pl. Rar. 2:1. 1844.
Brochosiphon Nees in Alph. de Candolle, Prodr. 11:492. 1847.
Dactylostegium Nees in Martius, Fl. Brasil. 9:162. 1847.

Perennial herbs or shrubs with cystoliths; young stems usually ± distinctly 6-angled in cross-section. Leaves opposite, entire to subsinuate. Inflorescence of axillary cymes (= modified dichasia ?) bearing 1 or more, bracteolate cymules; cymes subtended by paired bracts, sessile or pedunculate in leaf axils or in axils of inflorescence bracts forming a terminal spikelike thyrse or panicle of thyrses; cymules sessile or pedunculate, comprising an involucre of several pairs of bracteoles, outermost pair usually conspicuous and larger than inner (often hyaline) pair(s), outer cymule bracteoles of a pair equal or unequal in size. Flowers 1-several per cymule, sessile. Calyx 5-lobed, usually reduced and hyaline, lobes equal to subequal in size. Corolla often resupinate (i.e., tube usually twisted 180° or rarely 360°), pink to purple, red, orange, yellow, white, or blue, often with pink to purple markings, tube cylindric to gradually expanded distally but generally lacking a distinct throat, limb 2-labiate, upper lip entire to 2-fid, lower lip entire to shallowly 3-lobed (normal position of lips reversed when corolla resupinate 180°), corolla lobes ascending-cochlear in bud. Stamens 2, exserted from mouth of corolla or rarely included in corolla tube; anthers 2-thecous, thecae of a pair equal to subequal in size, parallel to perpendicular, equally to unequally inserted or superposed on filament, usually lacking basal appendages (rarely with lower theca minutely

appendaged at base); pollen 3-colporate, 6-pseudocolpate; staminodes 0. Capsule substipitate to stipitate, retinacula present, septa with attached retinacula separating and rising from inner wall of mature capsule (i.e., septa elastic). Seeds 2 (or fewer by abortion) per valve, discoid.

Although about 300 species have been described from tropical and temperate regions of both the New World and the Old World, the number of species usually cited is about one-half that number or fewer. The genus pertains to subfamily Acanthoideae, tribe Justicieae, subtribe Diclipterinae (McDade et al. 2000).

Dicliptera verticillata (Forssk.) C. Chr., Dansk Bot. Ark. 4(3):11. 1922. *Dianthera verticillata* Forssk., Fl. Aegypt.-Arab. 9. 1775. *Justicia cuspidata* Vahl, Symb. Bot. 2:9, 16. 1791, nom. illegit. TYPE.— YEMEN. Without locality, *P. Forsskal 393* (lectotype, designated by Wood et al., Kew Bull. 38:450. 1983: C; possible isolectotype: BM).

Dicliptera umbellata (Vahl) Juss., Ann. Mus. Hist. Nat. Paris 9:268. 1807. *Justicia umbellata* Vahl, Enum. Pl. 1:111. 1804.

Dicliptera micranthes Nees in Wallich, Pl. As. Rar. 3:112. 1832.

Perennial herbs to 1.2 dm tall, often rooting at nodes; young stems hexagonal, internodes generally glabrous proximally and sparsely pubescent distally with trichomes ± restricted to ridges, trichomes retrorse and 0.2–0.3 (–0.6) mm long or flexuose and up to 1 mm long. Leaves opposite, petiolate, petioles to 33 (–50) mm long, blades (broadly ovate to) ovate to ovate-elliptic, 19–90 mm long, 4–46 mm wide, 1.5–3.5 × longer than wide, acute to acuminate at apex, (truncate to rounded to) acute at base, surfaces sparsely pubescent with trichomes ± concentrated on or restricted to major veins, margin entire, ciliolate. Inflorescence of axillary cymes of cymules; cymes alternate or opposite at nodes, 1–2 (–3) per axil, short pedunculate (peduncles 0.5–3 mm long), bracts subtending cymes subulate to lance-subulate to narrowly elliptic to subfoliose, 3–10 mm long; cymules (1–) 2–3 (–5) per cyme, sessile to pedunculate, peduncles to 3 mm long. Outer cymule bracteoles (ovate-elliptic to elliptic to) obovate, 5–10.3 (–17) mm long, 1.4–3.7 (–5) mm wide, those of a pair subequal to unequal in size (longer one 1.1–1.7 × as long as shorter one), conspicuously venose, apically mucronate to aristate (mucro 0.3–1.5 mm long), abaxial surface pubescent with an overstory of erect to flexuose eglandular trichomes to 1.3 mm long and an understory (sometimes absent) of eglandular, subglandular, and glandular trichomes 0.05–0.2 mm long, margin conspicuously ciliate with trichomes like those of abaxial surface. Inner cymule bracteoles ± fused at base, lanceolate (to lance-elliptic to narrowly elliptic), ± conduplicate, 6–8 mm long, hyaline proximally, apically prominently attenuate-aristate, abaxial surface pubescent with glandular and eglandular trichomes. Calyx 3.3–4.2 (–5) mm long, lobes subequal in size, abaxially pubescent like inner cymule bracteoles. Corolla dark pink with white patch on lower lip, resupinate 90° (i.e., corolla appearing on its side, with lips facing right and left rather than up and down) or apparently sometimes 180°(see discussion), 7–9 (–17) mm long, externally pubescent with ± flexuose eglandular trichomes 0.1–0.3 mm long, tube 4–5 (–7) mm long, 3-lobed lip 3–4.8 (–9.5) mm long, lobes 0.2–0.6 mm long (the central lobe largest), entire to emarginate lip 3–4.8 (–9.5) mm long. Stamens 3.5–5.5 (–9) mm long; thecae 0.3–0.7 mm long, those of a pair subequal to equal in size, parallel to perpendicular, superposed (touching); pollen (fig. 6D–F) 3-colporate, 6-pseudocolpate, interapertural exine reticulate. Style 6–8 (–15) mm long, glabrous. Capsule 4.5–5.1 (–6) mm long, pubescent with erect to flexuose eglandular and glandular trichomes 0.05–0.2 mm long. Seeds 1.2–1.5 mm long, 1.2–1.5 mm wide, surface and margin covered with conical tubercles to 0.1 mm long bearing retrorse barbs. Figure 2E.

ILLUSTRATION.— Heine (1966:199, Fig. 41).

Phenology.— Flowering and fruiting: April, July–September.

Distribution and habitats.— Widely distributed in tropical Africa (including: Angola, Cameroon, Cape Verde, Congo-Brazzaville, Equatorial Guinea [Annobón], Gabon, Gambia, Ghana, Ivory Coast, Malawi, Mali, Niger, Nigeria, São Tomé and Príncipe, Senegal, Sierra Leone, Tanzania, Togo) and in tropical Arabia; in São Tomé and Príncipe, plants occur in secondary forests, along beaches above the high tide line, in cacao plantations, along trails, and in moist roadbanks at elevations from sea level to 550 m.

Notes.— Although most collections of *D. verticillata* from São Tomé and Príncipe are morphologically homogeneous, a collection from São Tomé (*Figueiredo 208*) differs from the others in several conspicuous features, which are summarized in the following couplet:

1. Trichomes of distal internodes retrorse, 0.2–0.3 (–0.6) mm long; leaf blades acute at base; outer cymule bracteoles obovate, 5–10.3 mm long, 1.4–3.7 mm wide, those of a pair subequal to unequal in size (longer one 1.1–1.5 × as long as shorter one); calyx 3.3–4.2 mm long; corolla resupinate 90°, 7–9 mm long; stamens 3.5–5.5 mm long; capsule 4.5–5.1 mm long . . . . . Most Collections

1. Trichomes of distal internodes flexuose, to 1 mm long; leaf blades rounded to truncate at base; outer cymule bracteoles ovate-elliptic to elliptic to obovate, 6–17 mm long, 2–5 mm wide, those of a pair unequal in size (longer one 1.3–1.7 × as long as shorter one); calyx 5 mm long; corolla apparently resupinate 180°, 15–17 mm long; stamens 8–9 mm long capsule 5.5–6 mm long . . . . . *Figueiredo 208*

Superficial examination of specimens identified as *D. verticillata* from elsewhere in Africa reveal that in some regions (e.g., Cape Verde, Mozambique, Cameroon) plants showing similarities to *Figueiredo 208* (e.g., larger cymule bracteoles and corollas) are included within the variation of this species. Whether this reflects morphological variation within a single species or the presence of additional taxa remains to be addressed by subsequent studies of African *Dicliptera*. Heine (1963, 1966) included names in addition to those noted above within the synonymy of *D. verticillata*.

Corollas of *Daniel 11122* are "half resupinate." They are rotated 90°, with a slight twist in the distal portion of the corolla tube, so that the corolla appears to be on its side. The upper lip is entire to slightly 2-lobed and larger than the 3-lobed lower lip. Stamens are ± appressed to the upper lip and the anthers dehisce either toward the lower lip (i.e., flower nototribic) or toward each other (i.e., flower pleurotribic). This trait was maintained in plants of *Daniel 11122* cultivated in San Francisco from seeds. Corollas of *Figueiredo 208* appear (on the pressed herbarium specimen) to be resupinate 180° with the upper lip 3-lobed and the lower lip entire.

Additional specimens examined.— **Príncipe**: Sundi, *T. Monod 12073* (COI). **São Tomé**: along road (EN-2) at Praia Morrão, just N of Ribeira Afonso, ca. 21 km S of São Tomé, 00°12.113′N, 006°42.364′E, *T. Daniel 11122* (BR, CAS, K, MO, STPH, US); ca. 2.5–3 km (air) SE of Ponta Figo toward Pico São Tomé, at and ca. 0.5 km from Resevoir Centrale Hydroélectrique, 00°19.050′N, 006°33.005′–33.013′E, *T. Daniel 11146* (CAS); along road (EN-1) ca. 1 km NE of Neves, ca. 0.5 km E of tunnel, 00°21′39.05″N, 006°34′02.41″E, *T. Daniel 11190* (CAS, MO, STPH); Santa Catarina, Rio Contador, *J. Espírito Santo 4648* (LISC); Rio Contador, entre o fim do trilho dos túneis, junto ao Tanque, e o túnel no. 8, *E. Figueiredo 208* (LISC); Caue, Illot de Roles, *N. Garcia 21/Nu* (COI); Uba-Budo, Pedroma, 00°16′35″N, 006°42′00″E, *C. de Matos & K. van Essche 7515* (BRLU, LISC, STPH) ; Diana, 00°19′45″N, 006°41′00″E, *T. Stévart & F. de Oliveira 23* (BRLU, BR, STPH); Cascata (00°18′00″N, 006°33′30″E), *T. Stévart & F. de Oliveira 144* (BRLU).

Elytraria Michx., Fl. Bor.-Amer. 1:8. 1803, nomen conserv.

TYPE.— *Elytraria virgata* Michx., nomen illegit.

(≡ *Elytraria caroliniensis* (J.F. Gmel.) Pers.; *Tubiflora caroliniensis* J.F. Gmel.).

Tubiflora J.F. Gmelin, Syst. Nat. 2:27. 1791, nom. rej.

Annual to perennial herbs or shrubs lacking cystoliths. Leaves alternate or whorled, mostly in basal rosettes or crowded at apices of branches, sometimes ± diffuse along stems, entire to crenate to pinnatifid. Inflorescence of scapose or pedunculate densely bracteate axillary and terminal dichasiate spikes, scapes or peduncles covered with coriaceous clasping scales; dichasia 1-flowered; flowers subtended by 2 bracteoles. Calyx 4 (–5)-lobed, mostly hyaline, lobes heteromorphic, anterior and posterior lobes external, anterior lobe 2-dentate to ± deeply 2-cleft. Corolla pinkish, blue, white, or yellow, often with colored markings near mouth, tube cylindric or slightly expanded near mouth, limb 2-labiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes often apically divided or 2-cleft, descending-cochlear in bud. Stamens 2 (–4), included in tube or partially exserted from mouth of corolla; anthers 2-thecous, thecae of a pair (sometimes covered by stigma during anthesis) equal in size, parallel, equally inserted, lacking basal appendages; pollen generally 3-colpate; staminodes 0–2, minute. Capsule estipitate, subconic to ovoid, sometimes irregularly constricted proximally, retinacula absent. Seeds 5–13 (or fewer by abortion) per valve, irregularly shaped (often blocky or cubelike), lacking trichomes.

Twenty-two species occur in the tropics and subtropics of both the Old World (Africa, Madagascar, Indian Subcontinent) and the New World (North America, West Indies, Central America, South America). The genus is monophyletic and pertains to subfamily Nelsonioideae (Wenk and Daniel 2009).

Elytraria marginata Vahl, Enum. Pl. 1:108. 1804. TYPE.— "ad Senegal, in Guinea. *Thonning*," (holotype: C?). Although Vollesen (2008) indicated that he had seen the Thonning collection at C, I did not locate a specimen in the Isert & Thonning herbarium at C under this name in 2009. In addition to noting that the whereabouts of the holotype were unknown, Hepper (1976) also indicated that Vahl's mention of Senegal was likely an error.

Tubiflora paucisquamosa De Wild. & T. Durand, Bull. Soc. Roy. Belgique 38:42. 1899.

Caulescent unbranched or 1–2-branched annual herbs to 3 dm tall, lacking a basal caudex; young stems ± flattened (dried), sparsely pubescent with flexuose-crinkled erect to appressed eglandular trichomes 0.2–0.5 mm long. Leaves in 1–3 (or more?) clusters or whorls along and/or at apex of stems, (3–) 6–11 per node, petiolate, petioles (naked portion) to 8 mm long, blades elliptic (to obovate-elliptic), (14–) 38–141 mm long, (7–) 10–43 mm wide, 1.8–4.2 × longer than wide, acute to rounded-acute at apex, long attenuate at base (often tapering nearly to node), surfaces pubescent (trichomes ± restricted to veins) with cauline type trichomes to 1 mm long, margin entire to subsinuate, sparsely ciliate. Inflorescence of 1–5 pedunculate spikes that are possibly terminal (when solitary) or terminal and/or axillary when more than 1, inflorescence(s) subtended by clusters or whorls of leaves (and when present, subsequent vegetative growth apparently sympodial and overtopping inflorescence(s)), peduncles 13–90 mm long, scales spirally arranged, remote and sparse (either not imbricate or only so distally), ovate to broadly ovate, conduplicate-clasping, 2.2–4 mm long, 1.5–2.4 mm wide, apex mucronate, mucro 0.2–0.6 mm long, margin whitish and ciliate, abaxial surface glabrous, spikes 15–155 mm long, 4–8 mm in diameter near midpoint, rachis pubescent with flexuose-crinkled eglandular trichomes to 1 mm long. Bracts clasping, ovate to broadly ovate, 4–5.2 mm long, 2.4–3 mm wide, apex mucronate, mucro 0.7–1 mm long, margin

whitish and ciliate with acropetally directed ± flexuose trichomes to 0.5 mm long, abaxial surface glabrous. Bracteoles positioned near edges of posterior calyx lobe and conduplicate there, narrowly elliptic to linear to lance-linear, often hyaline from margin to near midvein, 3–3.2 mm long, 0.6–0.9 mm wide, abaxially pubescent along midvein with flexuose-crinkled and ± acropetally directed eglandular trichomes to 0.5 mm long, margin ciliate. Calyx 3.5–4.2 mm long, lobes and divisions mucronate at apex, abaxially glabrous, margins distally ciliate, anterior lobe ± elliptic to elliptic-obovate, 2.5–3.5 mm long, 1–1.5 mm wide, divided 0.73–0.91 its length, divisions lance-linear, 2.2–3 mm long, posterior lobe ovate to ovate-elliptic, 2.9–3.3 mm long, 1.4–1.8 mm wide, lateral lobes linear-lanceolate to linear-elliptic, 2.5–3.4 mm long, 0.9–1 mm wide. Corolla entirely white, 4–5 mm long, externally glabrous, tube internally rugulate on posterior side, subcylindric to gradually expanded distally, 1.5–2.2 mm long, 0.6–1 mm in diameter near midpoint, upper lip ± curved downward so that there is relatively scant opening of corolla between the lips, 2–2.5 mm long, apically 2-lobed, lobes 0.2–0.6 mm long, lower lip 2.2–3 mm long, lobes 0.5–1.5 mm long, 0.7–2.4 mm wide, lateral lobes broadly elliptic, central lobe linear to ± oblate (up to 2 × as wide as long), apically emarginate. Stamens 2, exserted from mouth of corolla, 1.2–2.5 mm long; filaments 1.3–1.8 mm long, pubescent with subsessile to stipitate glandular trichomes to 0.05 mm long; thecae 0.4–0.9 mm long, subequal, parallel, glabrous; staminodes 2, peglike, 0.1–0.2 mm long; pollen (fig. 6G–I) 3-colpate, interapertural surfaces reticulate. Style 2–2.4 mm long, glabrous; stigma obovate-spatulate, 1.5 mm long, 0.5 mm wide. Capsules conic (sometimes constricted proximally), 3.5–4.3 mm long, glabrous. Seeds up to 26 per capsule [ovules 11–13 per valve, mature seeds 8–12 per capsule in cultivated plants of *Daniel 11158*], ± blocky to reniform, 0.3–0.6 mm long, 0.4–0.7 mm wide, surface coarsely reticulate and covered with blunt to pointed papillae < 0.05 mm long. Figure 4A–B.

Illustrations.— Morton (1956:55, fig. 2); Heine (1966:157, fig. 31); Lisowski (2009:2, fig. 6).

Phenology.— Flowering and fruiting: December–September.

Distribution and habitats.— Widely distributed in tropical western and central Africa (Angola, Congo-Kinshasa, Cameroon, Equatorial Guinea (Bioko, Río Muni), Gabon, Ghana, Ivory Coast, Liberia, Nigeria, São Tomé and Príncipe, Sierra Leone, Sudan, Togo, Uganda; plants occur in secondary forests and in disturbed areas (along trails and roads, in plantations), where they are sometimes weedy. The species occurs on each of the major islands in the Gulf of Guinea except Annobón. Plants on both São Tomé and Príncipe occur in disturbed areas of moist to wet montane forest and swamps at elevations from 8 to 570 m.

Local names.— "Focha anzolo" (*Quintas 1079*), "santage-bassocafé" (*Espírito Santo 4534*).

Notes.— The taxonomy of *Elytraria* in Africa has received considerable attention and is currently under review using both morphological and molecular lines of evidence.

Exell (1944) included *E. marginata* within the widespread *E. acaulis* (L.f.) Lindau. Morton (1956) and subsequently Dokosi (1971, 1979) recognized numerous African species, including *E. marginata*.

Additional specimens examined.— **Príncipe**: vicinity of Santa Trindade (= Roça Pico Papagaio) at N slope of Pico Papagaio, between Esperança and São Joaquim (Oeste), 01°37.156′N, 007°23.540′E, *T. Daniel 11158* (CAS, K, STPH); Esperança, *A. Exell 690* (COI, K); S. Joaquim, Praia Caixão, 01°37′04″N, 007°22′07″E, *F. Oliveira 530* (BRLU, STPH); entre Rio Banzó–Pico João Dias Pai e João Dias Filho, *F. Oliveira 136/98* (STPH); Santa Trindade, at base of Pico Papagaio, *J. de Wilde et al. 425* (WAG). **São Tomé**: Roça Monte Café, *A. Moller 172* (COI); Roça Rodia, *A. Moller 584* (COI); prox. a S. Thomé, *A. Moller 666* (COI); Roça Vale Carmo to Guaiaquil (00°10′N, 06°31′E), *F. de Oliveira 1351* (BRLU); Angolares at Pesqueira de Deus, *F. Quintas 1079* (COI); Corrêa, *F. Quintas 1190* (COI), *s.n.* (LISU); without locality, *Seabra s.n.* (COI); Parc Nat. d'Obo, Rio Xuf Xuf, 00°08′30″N, 006°30′15″E, *T. Stévart & F. de Oliveira 151*

(BRLU, STPH); plantation Ribeira Peixe, N.W., track leading from Mateus Sampaio to Monte Carmo, *J. de Wilde et al. 180* (WAG). **Island unknown**: without locale, *J. Espírito Santo 4534* (LISC); without locale, *F. de Oliveira s.n.* (LISC).

Heteradelphia Lindau, Bot. Jahrb. Syst. 17:108. 1893.

TYPE.— *Heteradelphia paulowilhelmia* Lindau.

Shrubs with cystoliths. Leaves opposite, crenate to crenate-dentate. Inflorescence of terminal dichasiate thyrses or panicles; dichasia usually 3- to many-flowered; flowers subtended by 2 bracteoles; bracts and bracteoles often caducous. Calyx 5-lobed, lobes subequal to unequal in size. Corolla purplish red or maroon-purple, tube elongate, distally expanded into a ± distinct throat, limb subactinomorphic, subequally 5-lobed, lobes left-contorted in bud. Stamens 4, exserted (at least partially) from mouth of corolla but not or only slightly extending beyond limbs; anthers 2-thecous, thecae of a pair equal in size, parallel, equally to unequally inserted, lacking basal appendages; pollen 3-porate, 12-pseudocolpate, pores flanked by 2 ± curved liplike regions of exine; staminodes 0. Capsule linear-ellipsoid, substipitate, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic). Seeds 6–7 (or fewer by abortion) per valve, discoid, sometimes with hygroscopic trichomes on margin.

Two species of *Heteradelphia* are currently recognized. Clarke (1899a:54) indicated that Lindau had distinguished his new genus from *Paulowilhelmia* Hochst. by "the approximation of the two membranes whence the lateral pair of stamens spring. The difference in the shape of the corolla would be a stronger reason for separating it generically; but the enormous differences in size and shape of the corolla in allied genera (as in *Ruellia*) do not dispose to attributing much weight even to that character." Indeed, although both genera have been recognized since Clarke's account (e.g., Exell 1944, 1973; Scotland and Vollesen 2000), the distinctions between them are not well established based on morphological traits. Molecular studies should assist in determining whether *Heteradelphia* should be treated as distinct from *Eremomastax* Lindau (including *Paulowilhelmia*). Both genera pertain to subfamily Acanthoideae, tribe Ruellieae.

For more than 50 years *Heteradelphia* was thought to be a unispecific genus that was endemic to São Tomé. A second species (*H. paulojaegeria* Heine) occurring in mainland Africa (Guinea, Ivory Coast, Niger, Sierra Leone) was described in 1961. Molecular studies might help to determine whether the two species of *Heteradelphia* are monophyletic. They may be distinguished from one another by the characteristics in the following couplet:

1. Corolla 65–79 mm long; seed surfaces scabrous to ± warty roughened and covered with trichomes or trichomelike papillae to 0.05 mm long, margin neither thickened nor bearing conspicuous hygroscopic trichomes; plants of São Tomé ..... *H. paulowilhelmia*
1. Corolla 40 mm long; seed surfaces ± scaly but lacking trichomes or trichomelike papillae, margin thickened and covered with appressed hygroscopic trichomes (to 1 mm long when moistened); plants of mainland Africa ..... *H. paulojaegeria*

Heteradelphia paulowilhelmia Lindau, Bot. Jahrb. Syst. 17:109. 1893. *Paulowilhelmia nobilis* C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. 5:53. 1899. TYPE.— SÃO TOMÉ AND PRÍNCIPE. São Tomé: Macambrará, 1200 m, Jun 1885 [flr, frt], *A. Moller 86* (lectotype, designated here: COI!; isolectotype: K!).

Stout to weak shrubs to 2 m tall; young stems quadrate-sulcate, either 1) pubescent with flexuose multi-septate eglandular trichomes to 0.2 mm long, these either evenly disposed (e.g., *Espírito Santo 4488*) or concentrated in to ± restricted to 2 lines (most collections) or 2) densely and

evenly pubescent with ± crinkly multi-septate eglandular trichomes 0.2–1 (–1.5) mm long. Leaves petiolate, petioles to 100 mm long, blades ovate, 20–185 mm long, 14–120 mm wide, 1.3–2.4 × longer than wide, acuminate and often falcate at apex, rounded to subcordate at base, surfaces either 1) pubescent with flexuose to appressed multi-septate eglandular trichomes to 0.7 mm long, the trichomes mostly restricted to major veins or 2) pubescent with cauline type trichomes, the trichomes not restricted to major veins (at least on adaxial surface, often on abaxial surface as well), abaxial surface purplish or green, margin coarsely and irregularly dentate-crenate. Inflorescence of terminal, sessile to pedunculate, and leafy dichasiate thyrses to 31 cm long (including peduncle, if present), these sometimes borne on short axillary shoots and branching, thus appearing as a panicle with axes bearing dichasia, lower branches sometimes abortive, rachis pubescent like young stems and (at least distally) also with erect to flexuose glandular trichomes 0.1–2.3 mm long (these rarely inconspicuous); dichasia expanded, 3- or more-flowered, pedunculate, peduncles 17–50 mm long, pubescent like rachis (or with glands more numerous), secondary peduncles similar to peduncles except usually shorter. Bracts ± caducous, foliose proximally and reduced in size distally, 12–45 mm long, 5–20 mm wide, pubescent like leaves and often with glandular trichomes as well. Bracteoles subfoliose, petiolate, elliptic to obovate, 6–13 mm long, 2.5–5 mm wide, pubescent like leaves or with glandular trichomes as well, secondary bracteoles similar to bracteoles except smaller. Flowers subsessile to pedicellate, pedicels to 2 mm long. Calyx 19–27 (–34 in fruit) mm long, lobes sometimes maroon, linear to lanceolate, 16–25 (–32 in fruit) mm long, 1.3–2.1 mm wide (widest at or above base), subequal to unequal in length, apically rounded or slightly expanded and rounded to subacute, abaxially pubescent with understory of antrorse to appressed eglandular trichomes 0.1–0.3 mm long (sometimes absent) and an overstory of flexuose to erect glandular trichomes 0.1–2 mm long. Corolla maroon-purple to purple-violet (with lobes darker than tube), 65–79 mm long, externally glabrous (or with a few glandular and eglandular trichomes to 0.5 mm long on throat), tube arched, 48–65 mm long, expanded distally into a ± distinct throat, narrow proximal portion 45–50 mm long, throat 10–14 mm long, limb subactinomorphic, 28–43 mm in diameter, upper lip 12–16 mm long, lobes 9–13 mm long, 10–12 mm wide, lower lip 14–20 mm long, lobes 10–15 mm long, 9.5–15 mm wide, apically emarginate. Stamens with longer pair 16 mm long, shorter pair 12 mm long; thecae 3–4.9 mm long, presented at ± same height or at 2 different heights; pollen (fig. 7A–B) 3-porate, 12-pseudocolpate, pores flanked by 2 ± curved lip-like portions of exine, interapertural exine reticulate. Style 53–78 mm long, pubescent ± throughout with antrorse eglandular trichomes; stigma recurved, 1.5–2 mm long, only 1 lobe evident; ovary pubescent apically. Capsule linear-ellipsoid, 15–24 mm long, proximally glabrous, distally glabrous or pubescent with erect eglandular trichomes 0.1–0.2 mm long (sometimes restricted to apex). Seeds 2.5–2.6 mm long, 1.7–2.6 mm wide, surfaces ± warty roughened and covered with erect trichomes or trichomelike papillae to 0.05 mm long (scabrous). Figure 3C–D.

Illustrations.— None found.

Phenology.— Flowering: April–December; fruiting: April–September.

Distribution and habitats.— Endemic to São Tomé where plants occur along trails in moist to wet montane primary (or secondary) forests at elevations of (1000–)1180–1500 m and on the bog mat at Lagoa Amélia at an elevation near 1400 m.

Conservation.— This narrow endemic occurs only between 1000–1500 m on São Tomé. The bog mat form (see below) occurs only on Lagoa Amélia whereas the typical (forest) form becomes abundant along trails between these altitudes. Even though the species does not seem to be particularly rare, its limited distribution makes it vulnerable. At the present time, its habitat is partially within the protected Parque Natural Obô. The species is worthy of cultivation for both the habit and foliage of the typical (forest) form and the large purplish flowers.

NOTES.— The holotype of *Heteradelphia paulowilhelmia* was destroyed at B. A lectotype is designated from the remaining known original materials at COI and K. The complete specimen at COI bears three numbers (86, 378, and 198) and the locality data as noted above. Exell (1944) discussed the numbering and distribution of Moller's collections from COI. The isotype at K (ex B) consists of fragments in a packet mounted on a sheet with a packet containing fragments of *Mann 1094*.

Clarke (1899a) included *Heteradelphia paulowilhelmia* under *Paulowilhelmia*, as *P. nobilis* C.B. Clarke. He noted that neither differences in shape of the corolla nor insertion of the stamens justify the recognition of *Heteradelphia* as distinct from *Paulowilhelmia* (= *Eremomastax*). Clarke (1899a) also indicated that seeds of *H. paulowilhelmia* have hygroscopic trichomes on the margin. Hygroscopic trichomes were not evident on a single seed of *Espírito Santo 4026* that was immersed in water. Figure 8 shows a dry seed of this species with magnification of its surface ornamentation. Conspicuous hygroscopic trichomes were detected on seeds of *H. paulojaegeria* from mainland Africa.

The inflorescences, flowers, and fruits of all collections of *H. paulowilhelmia* appear remarkably consistent. However, two forms, apparently differing only in vegetative characteristics, are evident among the specimens examined. Although both forms grow at moderately high elevations in a region of moist to wet forest, their habitats appear to be distinctive. Weaker and more densely pubescent plants with leaves possessing a purplish coloration occur on the floating bog mat that covers Lagoa Amélia (Fig. 9B). Stouter shrubs with less pubescence and larger leaves that lack a purplish tinge occur along trails on the forested slopes above and below the lake (Fig. 9A). The type of *H. paulowilhelmia* pertains to the less pubescent (forest) form. Plants conforming to the "bog mat form" are represented by *Daniel 11137*, *Exell 385*, *Joffroy 5*, and *Monod 11762*. The two forms of this species can be distinguished by the characters summarized in the following couplet:

1. Stout and erect shrubs to 2 m tall; young stems pubescent with flexuose multi-septate eglandular trichomes to 0.2 mm long, these either evenly disposed (e.g., *Espírito Santo 4488*) or concentrated in to ± restricted to 2 lines (most collections); leaves with petioles to 100 mm long, blades 60–185 mm long, 25–120 mm wide, surfaces pubescent with flexuose to appressed multi-septate eglandular trichomes to 0.7 mm long, trichomes mostly restricted to major veins, abaxial surface not purplish. ..... Typical (forest) form
1. Weak shrubs to 1.5 m tall; young stems densely and evenly pubescent with ± crinkly multi-septate eglandular trichomes 0.2–1 (–1.5) mm long; leaves with petioles to 25 mm long, blades 20–84 mm long, 14–39 mm wide, surfaces pubescent with cauline type trichomes, trichomes not restricted to major veins (at least on adaxial surface, often on abaxial surface as well), abaxial surface usually purplish. ..... Bog mat form

ADDITIONAL SPECIMEN EXAMINED.— **São Tomé**: without locality, *E. Campos 6* (COI); between Monte Café and the Pico, *A. Chevalier 13681* (K) [specimen says "Port Allègre sud de l'île" but Exell (1944) noted that he suspects that this is incorrect and that the locality is correctly stated in Sudania 2:35. 1914, where the number is miscited as "16681."]; trail from Jardim Botânico de Bom Sucesso (00°16.866′N, 006°38.868′E) to Lagoa Amélia (00°15.972′N, 006°35.589′E), *T. Daniel 11137* (CAS, K, MO, STPH); trail from Jardim Botânico de Bom Sucesso (00°16.866′N, 006°38.868′E) to Lagoa Amélia (00°15.972′N, 006°35.589′E), *T. Daniel 11139* (CAS); Monte Café, Esperança, *J. Espírito Santo 4026* (COI); M. Café–S. Pedro, *J. Espírito Santo 4488* (LISC); M. Café–Esperança, *J. Espírito Santo 4608* (LISC); Lagôa Amélia, crater-swamp, *A. Exell 385* (BR, COI, K); Me Zochi, Lagoa Amélia, *N. Garcia 60/Nu* (COI); Macambrará, 00°16.75′N, 006°36.80′E, *G. Joffroy 1* (BRLU); Lagoa Amélia, fond du cratère, 0°16.95′N, 6°35.80′E), *G. Joffroy 5* (BRLU, STPH); chemin ver Calvário, 00°17′N, 006°37′E, *G. Joffroy 84* (BRLU, STPH); entre Bom Sucesso et Lagoa Amélia, 00°17′N, 006°36′E, *J. Lejoly 94/526* (BRLU, LISC, STPH); without locality,

G. Mann 1094 (K); entre Bom Sucesso et Lagoa Amélia, *C. de Matos & K. Van Essche 7302* (BRLU, LISC), *7303* (BRLU, LISC); entre Pico et Roça Ponta Figo, 00°16′N, 006°33′E, *C. de Matos & K. van Essche 7394* (BRLU, LISC, STPH); Bom Sucesso, *A. Moller 162* (COI); Macambrará, *A. Moller s.n.* (LISU); Lagoa Amélia, *T. Monod 11720* (COI); Lagoa Amélia, bord crater, *T. Monod 11762* (COI); Bom Sucesso–Lagoa Amélia, 00°17′N, 006°37′E, *F. de Oliveira 184* (STPH); antigo pomar ECOFAC, 00°16′N, 006°36′E, *F. de Oliveira 1449* (BRLU); Pico Calvário, *M. Rose 142* (K); Parc National d'Obo, Bom Sucesso, chemin Lagoa Amélia, 00°17′30″N, 006°36′45″E, *T. Stévart & F. de Oliveira 5* (BRLU); Parc National d'Obo, entre Pico de São Tomé and Pico Pequeno, 00°16′00″N, 006°32′30″E, *T. Stévart & F. de Oliveira 111* (BRLU).

Justicia L., Sp. Pl. 15. 1753, nom. cons.

LECTOTYPE (designated by Hitchcock and Green, International Botanical Congress, Cambridge (England), 1930: Nomenclature Proposals by British Botanists. 116. 1929).— *Justicia hyssopifolia* L.

Rhaphidospora Nees in Wallich, Pl. Asiat. Rar. 3:77, 115. 1832.
Rostellaria Nees in Wallich, Pl. Asiat. Rar. 3:76, 100. 1832, nom. illegit. (non Gaertner 1807).
Rostellularia Reichenb., Handbk. Nat. Pflanzensyst. 190. 1837.
Duvernoia E. Meyer ex Nees in Alph. de Candolle, Prodr. 11:322. 1847.
Anisostachya Nees in Alph. de Candolle, Prodr. 11:368. 1847.

Annual to perennial herbs, shrubs, or (rarely) trees with cystoliths. Leaves opposite, entire to crenate. Inflorescence of dichasia in leaf axils or of axillary or terminal dichasiate spikes, racemes, or thyrses, inflorescences sometimes branched and becoming panicles; dichasia 1–many-flowered; flowers subtended by 2 bracteoles. Calyx 4–5-lobed, lobes equal or unequal in size, posterior lobe sometimes greatly reduced in flowers with 5 calyx lobes. Corolla greenish, white, yellow, orange, pink, red, purple, or blue usually with white or colored markings (often restricted to lower lip) within, tube expanded from near base to expanded only distally or cylindric throughout, often lacking a distinct throat, limb strongly zygomorphic, 2-labiate, upper lip internally rugulate (i.e., with a stylar furrow), entire to 2-lobed, lower lip 3-lobed, corolla lobes ascending-cochlear in bud. Stamens 2, usually exserted from mouth of corolla; anthers 2-thecous (1 theca rarely sterile), thecae of a pair equal to unequal in size, parallel to perpendicular, equally inserted, unequally inserted (but overlapping for some portion of their length), or superposed (i.e., not overlapping), 1 or both with a basal appendage or sometimes appendages absent; pollen 2–4-aperturate (varying from porate to colporate), apertures flanked on each side by 1-several rows of ± circular insulae and/or peninsulae or by a pseudocolpus; staminodes 0 (although pubescent thickenings near attachment of filaments rarely present). Capsule stipitate, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic). Seeds 2 (or fewer by abortion) per valve, discoid to globose, rarely with trichomes.

Justicia is the largest genus of Acanthaceae with estimates of up to 700 species. It occurs in tropical and subtropical (to temperate) regions worldwide. Morphological diversity (especially floral form and color) in the genus is extensive, and the above generic description likely does not encompass all of the known variation. The generic synonymy noted above only includes genera in which taxa from São Tomé and Príncipe have been treated. Graham (1988) presented a comprehensive generic account of *Justicia* that includes many generic synonyms on a world-wide basis. The genus pertains to subfamily Acanthoideae, tribe Justicieae. Two species are known from São Tomé and Príncipe.

1. Annuals; young stems and leaf surfaces pubescent; leaf blades 1.4–2.6 × longer than wide; calyx 2.3–3 mm long, lobes heteromorphic (posterior lobe ½ or less as long as others); corolla 3 mm long ..... *J. tenella*

1. Perennials; young stems and leaf surfaces glabrous; leaf blades 2.7–4.2 × longer than wide; calyx 3–5.5 mm long, lobes ± homomorphic; corolla 7.5–9 mm long ..... *J. thomensis*

Justicia tenella (Nees) T. Anders., J. Proc. Linn. Soc., Bot. 7:40. 1863 ["1864"], non *J. tenella* Boerl. (1899). *Rostellularia tenella* Nees in Alph. de Candolle, Prodr. 11:369. 1847. *Anisostachya tenella* (Nees) Lindau in Engler & Prantl, Nat. Pflanzenfam. 4(3b):329. 1895. **Type.**— MADAGASCAR: "in pratis humidis inter saxa prov. Emirnae insulae Madagascar, *Bojer s.n.* (syntypes: G ex herb DC, K ex herb. Hook.); GUINEA: "in Senegambiâ secus fluvium Rio Nunez," *Heudelot 4* (syntype: P).

Rostellularia crenulata Nees in Alph. de Candolle, Prodr. 11:369. 1847.
Rostellaria parviflora Benth. in W. Hooker, Niger Fl. 481. 1849. TYPE.— SÃO TOMÉ AND PRÍNCIPE: São Tomé: without locality, *Don s.n.* (holotype: BM; isotype K!).
Rungia baumannii Lindau, Bot. Jahrb. Syst. 22:120. 1895.

Annual herbs to 2.5 dm tall, often rooting at nodes; stems horizontal to erect, young stems quadrate-sulcate, pubescent with retrorse eglandular trichomes (mostly or entirely restricted to 2 lines). Leaves petiolate, petioles to 16 mm long, blades ovate to elliptic to broadly elliptic, 9–39 mm long, 5.5–24 mm wide, 1.4–2.6 × longer than wide, (rounded to) acute at apex, acute to subattenuate at base, margin entire, ciliolate with antrorse eglandular trichomes to 0.1 mm long, surfaces sparsely pubescent (trichomes ± restricted to veins). Inflorescence of axillary pedunculate dichasiate spikes, peduncles to 25 mm long, spikes 1–4 per node, 6–25 mm long, 4.5–7 mm wide near midpoint, densely bracteate (rachis not visible) and 4-ranked, 2 adjacent ranks fertile and 2 adjacent ranks sterile, rachis ± sparsely puberulent with retrorse eglandular trichomes to 0.05 mm long; dichasia sessile, 1-flowered. Fertile bracts obovate to deltate, 3.5–5 mm long, 3.2–4 mm wide, rounded to truncate at apex, narrowed or constricted proximally into a stalk to 1 mm long, abaxial surface glabrous, sometimes pinkish along margin distally; sterile bracts similar to fertile bracts except smaller and sometimes asymmetric. Bracteoles lanceolate, 1.5–1.9 mm long, 0.2–0.3 mm wide, abaxial surface glabrous. Flowers sessile, not extending beyond bracts. Calyx 5-lobed (4+1), 2.3–3 mm long, lobes heteromorphic, posterior lobe elliptic to lance-triangular, 0.5–1 mm long, 0.1 mm wide, other 4 lobes lance-subulate, 2–2.5 mm long, 0.2 mm wide, lobes abaxially subglabrous or sparsely pubescent with antrorse eglandular trichomes (and rarely with glandular trichomes) less than 0.05 mm long, margin ciliolate with trichomes less than 0.05 mm long. Corolla white with pink to reddish markings on lower lip, 2.6–3 mm long, externally glabrous, tube 1.5–1.8 mm long, upper lip 1–1.4 mm long, apically entire, lower lip 1–1.5 mm long, lateral lobes 0.4 mm long, 0.3–0.4 mm wide, lower-central lobe 0.5 mm long, 0.7–0.9 mm wide. Stamens 1.5–1.7 mm long; thecae unequally inserted (overlapping for 0.1–0.2 mm), subperpendicular, 0.2–0.6 mm long (including basal appendage), unequal in length (proximal larger), glabrous, proximal theca with a spurlike or hornlike basal appendage 0.3 mm long; pollen (fig. 5I) 3-colporate, 6-pseudocolpate, interapertural surfaces reticulate. Style 1.3–1.5 mm long, glabrous or proximally pubescent with eglandular trichomes; stigma less than 0.1 mm long, lobes not evident. Capsule 2.9–3.2 mm long, glabrous proximally, beak with inconspicuous glandular trichomes to 0.05 mm long. Seeds 0.5–0.7 mm long, 0.4–0.7 mm wide, surfaces and margin pubescent with hygroscopic trichomes, trichomes appressed when dry and appearing 0.05 mm long, spreading when moistened and 0.1 mm long. Figure 2F.

Illustration.— Heine (1966:217, fig. 45, 9–15).

Phenology.— Flowering: December–August; fruiting: November–August.

Distribution and habitats.— This widely distributed Paleotropical species is known from

tropical Africa (Burundi, Cameroon, Central African Republic, Congo-Kinshasa, Equatorial Guinea [Bioko], Gabon, Ghana, Guinea, Guinea-Bissau, Ivory Coast, Liberia, Malawi, Mali, Mozambique, Nigeria, São Tomé and Príncipe, Senegal, Sierra Leone, Sudan, Tanzania, Togo, Zimbabwe) and Madagascar. In São Tomé and Príncipe plants occur in littoral regions, in disturbed areas (e.g., cacao plantations), and along streams in regions of moist to wet lowland and montane primary and secondary forests at elevations from 0 to 1470 m.

Notes.— The species was treated in *Justicia* sect. *Betonica* (Nees) T. Anders. subsect. *Anisostachya* (Nees) V.A.W. Graham by Graham (1988), who also noted that it is the only species of this subsection that occurs outside of Madagascar. Much of the above synonymy is based on Heine (1966), except that he also included *Aetheilema rupestre* Nees as a synonym of *J. tenella*. That name is the basionym of *Phaulopsis rupestris* (Nees) Lindau, a species recognized by Manktelow (1996) in a revision of *Phaulopsis*.

Corollas of *J. tenella* are among the smallest in the genus or in the family. Plants have a rapid generation time. Seeds obtained in April in São Tomé were planted in May in a greenhouse in San Francisco where the resultant plants were in full flower in the second week of July. Seeds have been noted to have hygroscopic trichomes (Graham 1988; Heine 1966), and our studies confirmed this (fig. 10). Contrary to their often common or diagnostic presence in other lineages of Acanthaceae, hygroscopic trichomes on seeds are rare among Justicieae.

Additional specimens examined.— **Príncipe**: without locality, *Barter 1985* (K); SE sector of island, near N base of Os Dois Irmãos, 01°34.889′N, 007°25.548′E to 01°35.728′N, 007°25.263′E, *T. Daniel 11179* (BR, CAS, K, MO, STPH, US); base W du Pico, *T. Monod 12174* (COI); entre Rio Banzó e Pico João Dias Pai e João Dias Filho, *F. Oliveira 135/98* (STPH). **São Tomé**: along road from Trindade to Bombaim, 13.4 km SW of jct. São Tomé-Bom Sucesso road, 00°15.270′N, 006°37.824′E, *T. Daniel 11188* (CAS, K, MO, STPH); along road between Santa Catarina and Praia Capito, ca. 2 km S of Sta. Catarina, 00°14.426′N, 006°28.294′E, *T. Daniel 11192* (CAS, STPH); Juliana de Sousa, *J. Espirito Santo s.n.* in March 1968 (LISC); entre Monte Castro (Murvillea) et Ponta Figo, 00°19′N, 006°33′E, *J. Lejoly 95/049* (BRLU, LISC, STPH); entre St. Miguel et Pico Zagaia, 00°10′N, 006°31′E, *C. de Matos & K. van Essche 7250* (STPH); le long du Rio Xufexufe, *C. de Matos & K. van Essche 7251* (BRLU, LISC); entre Pico et Roça Ponta Figo, 00°16′N, 006°33′E, *C. de Matos & K. van Essche 7393* (BRLU, LISC, STPH); Nova Moka, *A. Moller 69* (COI), *346* (COI), *487* (COI); Roça Saudade, *A. Moller 105* (COI); Angolares, *Newton s.n.* in April 1888 (COI); Io Grande, Rio Io Grande, 00°06′48″N, 006°38′32″E, *R. Odile 7* (BR); Burnay, 00°09′N, 006°29′E, *F. de Oliveira 416* (STPH); entre Buen Saiur [Buenos Aires] et Morro Miguel Ângelo, 00°14′N, 006°38′E, *F. Oliveira 108/98* (STPH); mata Monte Café cam S. Pedro, *F. Quintas 1130* (COI); S. Maria, *F. Quintas 1338* (COI); Nova Moka, *F. Quintas s.n.* (LISU); Monte Café, *F. Quintas s.n.* (LISU); Monte Café, *F. Welwitsch 5200* (K, LISU); SW coast, between Bindá and Juliana de Sousa, *J. de Wilde et al. 267* (WAG).

Justicia thomensis Lindau, Bot. Jahrb. Syst. 22:126. 1895. **Type.**— SÃO TOMÉ AND PRÍNCIPE. São Tomé: without locality or date, *J. de Sousa s.n.* (holotype: COI!; isotype: BM).

Perennials at least 2 dm tall; young stems subquadrate, glabrous. Leaves subsessile to petiolate, petioles to 4 mm long, blades ovate-elliptic to elliptic to obovate-elliptic, 20–46 mm long, 6–17 mm wide, 2.7–4.2 × longer than wide, acute at apex, acute to attenuate at base, margin entire, sparsely ciliate proximally with coarse and erect eglandular trichomes to 1 mm long, surfaces glabrous. Inflorescence of axillary or terminal subspicate axes of solitary flowers or dichasia in axils of subfoliose bracts, rachis glabrous; flowers or dichasia opposite, dichasia (when present) sessile to subsessile (i.e., peduncles to 0.5 mm long), 1 (or more?)-flowered. Bracts ± petiolate, elliptic, 6–12 mm long, 2.3–6.3 mm wide, apically rounded to subacute, abaxial surface glabrous (punctuate-glistening in light). Bracteoles absent or present, triangular to subulate, 0.3–1 mm long, 0.2–0.3 mm wide, abaxial surface glabrous. Flowers pedicellate, pedicels 0.5–1 mm long. Calyx

5-lobed, 3–5.5 mm long, lobes ± homomorphic, subulate to lanceolate, 4.2–4.8 mm long, 0.5–0.7 mm wide, abaxially glabrous, margin ciliate with eglandular trichomes 0.1–0.2 mm long. Corolla color unknown, 7.5–9 mm long, externally pubescent with an understory of glandular trichomes and an overstory of eglandular trichomes 0.05–0.2 mm long, tube 3–4.5 mm long, upper lip 3 mm long, lower lip 4–5 mm long, lobes of lower lip 1.5–2.8 mm long, 1.5–2.8 mm wide, central lobe largest. Stamens 5 mm long; thecae unequally inserted (overlapping for 0.5 mm), subparallel, 0.8–1.7 mm long (including basal appendage), unequal in length (proximal larger), distal theca dorsally pubescent with eglandular trichomes, proximal theca with a basal appendage 0.8 mm long; pollen unknown. Style 6 mm long, proximally pubescent with eglandular trichomes, distally glabrous; stigma 0.2 mm long, unequally 2-lobed. Immature capsule glabrous or with a few eglandular trichomes (to 0.2 mm long) at apex.

Illustration.— None found.

Phenology.— Although the type bears both flowers and young fruits, the date of collection was not recorded.

Distribution and habitats.— Endemic to São Tomé, but locale, habitat, and elevation for this species remain unknown.

Conservation.— This narrow endemic is either extremely rare or possibly extinct. Several collecting expeditions to São Tomé over the last fifteen years have not recollected this species, which is known from a single collection from the 19th century. It is a plant of major concern that should be considered critically endangered.

Notes.— The putative holotype, from the only known collection, of *J. thomensis* is fragmentary. The inflorescence appears complex and the interpretation of it presented above was formulated without dissection of the limited extant material. The specimen at COI is assumed to be the holotype; it was annotated as "Justicia thomensis n. sp." by Lindau and has been annotated as the holotype. However, Lindau did not cite an herbarium in the protologue, and it is possible that he had another specimen of de Sousa's collection (e.g., at B) that is no longer extant.

It is unclear why Lindau used the spelling "thomeensis" for the epithet of this species on both the putative holotype and in the protologue. Most authors have used "thomensis" for names based on plants from São Tomé (sometimes, especially formerly, spelled São Thomé); some recent authors of plant names have used the current spelling of the island's name, thus "tomensis." Although this epithet is not based on a Latin word or name, it must be treated as such according to the International Code of Botanical Nomenclature (McNeill et al. 2006). There would seem to be no basis for treating the "é" as part of the stem, and thus "thomeensis" would be an orthographical error to be corrected.

Hedrén (1988, 1989) treated *J. thomensis* in a morphologically delimited clade ("*Justicia capensis* species group") among an assemblage of putatively primitive species of *Justicia* sect. *Harnieria* (Solms-Laub.) Benth. Its putative relatives all occur in eastern Africa (e.g., Kenya, Tanzania, Mozambique, and eastern South Africa). A similar distribution pattern for relatives of various other organisms that are endemic to São Tomé has been noted (e.g., Drewes 2008).

Nelsonia R.Br., Prodr. 480. 1810.

Lectotype (designated by Bremekamp, ING card 00749. 1 Oct 1955).— *Nelsonia campestris* R.Br.

Annual to perennial usually low (often mat-forming) herbs lacking cystoliths. Leaves opposite (to alternate), entire. Inflorescence of axillary and terminal, densely bracteate dichasiate spikes; dichasia 1-flowered; flowers not subtended by bracteoles. Calyx 4-lobed, lobes heteromorphic, anterior lobe 2 (or more) cleft at apex, posterior lobe largest, lateral lobes enclosed by anterior and

posterior lobes. Corolla whitish (usually suffused with shades of pink or purple), tube ± constricted at apex, limb 2-labiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes descending-cochlear in bud. Stamens 2, partially exserted from mouth of corolla; anthers 2-thecous, thecae of a pair ± equal in size, parallel to ± divergent, equally (and basally) inserted, often with a subbasal flaplike appendage associated with dehiscence; pollen generally 3-colpate; staminodes 0. Capsule estipitate, subconic, retinacula absent. Seeds 4–14 (or fewer by abortion) per valve, subglobose to subellipsoid, one face somewhat flattened and with a shallow pore.

This pantropical genus is variously treated as consisting of a single variable species (e.g., Hossain 1984) or five species (e.g., Vollesen 1994, 2008). *Nelsonia* pertains to subfamily Nelsonioideae.

Nelsonia smithii Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:119. 1855. *Nelsonia canescens* (Lam.) Spreng. var. *smithii* (Oerst.) Hossain, Willdenowia 14:403. 1984. TYPE.— "Congo," *C. Smith s.n.* (holotype: C; isotype: BM).

Trailing (and rooting at nodes), distally ascendant herbs to 2.5 dm tall; young stems ± evenly pubescent with ± spreading and flexuose-crinkled eglandular trichomes 0.2–2 mm long. Leaves opposite, petiolate, petioles to 40 mm long, blades ovate to broadly ovate to elliptic, 10–85 mm long, 5.5–47 mm wide, 1.2–2 × longer than wide, acute to rounded at apex, abruptly attenuate to truncate to rounded at base, surfaces sparsely pubescent with flexuose to flexuose-crinkled eglandular trichomes to 1.5 mm long, margin entire and minutely scabrous-ciliate (trichomes < 0.05 mm long). Inflorescence of sessile (subtending leaves usually reduced in size, sometimes deciduous) to pedunculate densely bracteate spikes, peduncles to 6 mm long, pubescent with ± appressed to erect straight eglandular trichomes 0.6–1 mm long, spikes 10–45 mm long, 8–12 mm in diameter near midpoint, rachis pubescent with flexuose silky eglandular trichomes 1–2.5 mm long, trichomes often concentrated at nodes. Bracts broadly ovate to broadly elliptic, 5–7 mm long, 3–4.5 mm wide, acuminate to acute at apex, abaxial surface pubescent with a ± inconspicuous understory of sessile to stalked glandular trichomes 0.05–0.3 mm long and an overstory of straight eglandular trichomes 0.2–1 mm long, margin ± densely ciliate with straight to flexuose eglandular trichomes 0.8–1.5 mm long and an understory (sometimes sparse and inconspicuous) of glandular trichomes 0.05–0.5 mm long. Calyx 3.3–4.1 mm long, posterior lobe broadly elliptic to obovate-elliptic, 3.3–3.9 mm long, 1.6–2 mm wide, lateral lobes lanceolate to lance-elliptic, 2.5–3.4 mm long, 0.6–0.9 mm wide, anterior lobe elliptic, 3–3.8 mm long, 1.3–1.5 mm wide, apex 2-parted, divisions 0.5–0.7 mm long, 0.13–0.2 × as long as the anterior lobe, abaxial surface of calyx lobes pubescent with glandular trichomes 0.05 mm long and sparsely pubescent with an overstory of flexuose eglandular trichomes 0.5–2 (–3) mm long (longest trichomes concentrated near base), margin of lobes pubescent like abaxial surface or with eglandular trichomes sometimes denser. Corolla white with lobes pink (at least distally), 4–7 mm long, externally glabrous, tube 2.5–4 mm long, narrowest near midpoint, distally expanded into a throat 0.5–1.3 mm long, upper lip 1.2–2.5 mm long, 2-lobed, lobes 0.2–0.6 mm long, lower lip 1.2–3 mm long, lobes 0.6–2 mm long, 0.5–1.7 mm wide, internal surfaces of lower lip (proximal to lobes) and proximal portion of upper lip and distal portion of adjacent corolla tube pubescent with ± stiff brushlike eglandular trichomes to 0.3 mm long. Stamens inserted near base of corolla throat (i.e., within 1 mm of mouth of corolla), included in throat, 0.4–0.5 mm long; filaments inconspicuous, 0.2 mm long; thecae white, parallel, equally inserted, 0.2–0.3 mm long (up to 0.4 mm long including open basal flap), opening toward each other (flowers pleurotribic) by a basal flap 0.1 mm in diameter; pollen (fig. 7C–D) 3-colpate, interapertural surfaces reticulate. Style 1.5–2.7 mm long, glabrous; stigma included in corolla throat, presented

at ± same height as (and between) anthers, asymmetrically cupuliform or becoming ± unequally 2-lobed, 0.1–0.2 mm long. Capsule ovoid, 2.8–3.5 mm long, surface ± postulate-roughened, lacking trichomes or sometimes with inconspicuous sessile glands < 0.05 mm long especially near apex. Seeds up to 19 per capsule, often fewer, subhemispheric to compressed-globose, 0.2–0.3 mm long (high), 0.3–0.5 mm wide, surface covered with rounded to subconic papillae < 0.05 mm long. Figure 4E–G.

Illustrations.— Heine (1966:159, fig. 32); Vollesen (1994:317, fig. 1, K–L).

Phenology.— Flowering: November–April; fruiting: November, April.

Distribution and habitats.— Widespread in tropical Africa (Angola, Burundi, Cameroon, Central African Republic, Congo-Brazzaville, Congo-Kinshasa, Equatorial Guinea [Bioko], Ethiopia, Gabon, Ghana, Guinea, Ivory Coast, Liberia, Malawi, Nigeria, São Tomé and Príncipe, Senegal, Sierra Leone, Sudan, Tanzania, Uganda, Zambia,) where plants generally occur in regions of wet forests; in São Tomé and Príncipe plants occur in secondary forests and disturbed areas (e.g., cacao plantations, coastal *Pandanus* and palm forests above high tide line, forest trails, wet roadside swales) at elevations from near sea level to 440 m.

Notes.— Vollesen (1994) recognized five species of *Nelsonia*, three of which occur in Africa and nearby islands. His maps and distribution data indicate that both *N. canescens* and *N. smithii* occur on Bioko; however, neither was noted to occur on either Príncipe or São Tomé. *Nelsonia canescens* previously had been reported from Príncipe (Exell 1944, 1973), and plants of *Nelsonia* have been collected subsequently on São Tomé. Vollesen (1994) discussed in some detail the characters distinguishing these two species of *Nelsonia*, their respective habitat preferences, and a "blurring" between them in some regions caused by the spread of the weedy *N. canescens*. Others (e.g., Hossain 1984; Lebrun and Stork 1997) have treated *N. smithii* as a variety of *N. canescens*. Based on data provided by Vollesen (1994, 2008), the following couplet should permit identification of plants in this complex:

1. Plants trailing but not rooting at nodes, stems with a central taproot or caudex, pubescent with long (to 4 mm), thin, straight, non-collapsing trichomes; corolla tube (3–) 4–6 mm long; capsule glandular pubescent near apex; plants of various communities and often becoming weedy in disturbed habitats ..... *N. canescens*
1. Plants trailing and rooting at nodes, stems lacking a central taproot or caudex, pubescent with shorter, broad, curled, collapsing trichomes (occasional scattered thin hairs also sometimes present, especially distally); corolla tube 2.5–4 mm long; capsule glabrous throughout; plants of rain forests, never becoming weedy in other communities ..... *N. smithii*

Plants from both São Tomé (e.g., *Daniel 11125, 11186*) and Príncipe (e.g., *Daniel 11176*) conform rather well to *N. smithii* as treated by Vollesen (1994, 2008). They sometimes differ only in rather minor ways (e.g., *Daniel 11125* was weedy in the second growth of a cacao plantation, and *Daniel 11186* has capsules with minute glands at the apex). *Daniel 11180* from Príncipe possesses both types of cauline trichomes noted in the above couplet, with the *N. canescens*-type sometimes more prevalent than the *N. smithii*-type. Molecular studies of the taxa recognized in *Nelsonia* are currently underway, and might help to determine both the number of species that are worth recognizing and their phylogenetic relationships to one another.

Although the absence of bracteoles is a generic characteristic of *Nelsonia*, a few (likely teratological) bracteoles are very rarely present among plants from São Tomé (e.g., *Daniel 11186*). These are hyaline and inconspicuous (sometimes with a few green patches evident), subulate-linear, 4 mm long, 0.3 mm wide, and with eglandular trichomes to 1.5 mm long on the margin.

Additional specimens examined.— **Príncipe**: vicinity of mouth of Rio São Tomé and cove

ca. 1 km W on SW coast, 01°33′40.54″N, 007°21′15.51″E, *T. Daniel 11176* (CAS, K, MO, STPH); SE sector of island, near N base of Os Dois Irmãos, 01°34.889′N, 007°25.548′E to 01°35.728′N, 007°25.263′E, *T. Daniel 11180* (CAS, STPH); above Infante D. Henrique, *A. Exell 628* (COI), *639* (COI); Oquê Pipi, 01°24′N, 007°36′E, *F. de Oliveira 594* (BRLU, STPH). **São Tomé**: along road (EN-2) between São João dos Angolares and Porto Alegre, ca. 45 km S of São Tomé, 00°07.474′N, 006°37.988′E, *T. Daniel 11125* (CAS, K, MO, STPH); along road from Trindade to Bombaim, 13.4 km SW of jct. São Tomé-Bom Sucesso road, 00°15.270′N, 006°37.824′E, *T. Daniel 11186* (CAS, K, MO, STPH); Io Grande, Rio Io Grande, 00°06′48″N, 006°38′32″E, *R. Odile 20* (BR); Vale Carmo, *M. Ogonovszky 36* (BRLU); Vale Carmo, 00°09′08″N, 006°37′07″E, *F. de Oliveira 504* (BRLU, LISC); Roça Vale Carmo à Guaiaquil (00°10′N, 006°31′E), *F. de Oliveira 1345* (BRLU).

Phaulopsis Willd., Sp. Pl. 3:4, 342. 1800 ("*Phaylopsis*"), nom. et orth. cons.

TYPE.— *Phaulopsis parviflora* Willd., nom. illeg. (≡ *Micranthus oppositifolius* J.C. Wendl., *P. oppositifolia* (J.C. Wendl.) Lindau in Engler and Prantl, Nat. Pflanzenfam. Nachtr. II-IV 1:305. 1897, as "*oppositifolius*;" = *Phaulopsis dorsiflora* (Retz) Santapau).

Micranthus J.C. Wendl., Bot. Beobacht. 38. 1798, nom. rej.
Aetheilema R.Br., Prodr. Fl. Nov. Holl. 1:478. 1810.
Theileamea Baill., Bull. Mens. Soc. Linn. Paris 2:821. 1890.

Annual to perennial herbs with cystoliths. Leaves opposite, entire to crenate. Inflorescence complex, based on variably reduced dichasia, these sometimes conspicuously bracteate, densely clustered, and ± flattened; flowers subtended by bracteoles or not. Calyx 5-lobed, lobes unequal in size, posterior lobe larger than others. Corolla white to pink (sometimes with purplish markings on lower lip), tube straight to geniculate, ± expanded distally (sometimes into a distinct throat), limb 2-labiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes left-contorted in bud. Stamens 4, included in tube to at least partially exserted from mouth of corolla; anthers 2-thecous, thecae of a pair subequal in size, parallel, equally inserted, with or without basal appendages; pollen 3-porate (to 3-brevicolporate), 4–6 pseudocolpate, pores (or ora) flanked by 2 ± curved liplike protrusions of exine; staminodes 0. Capsule short stipitate, ± ellipsoid, retinacula present, septa with attached retinacula separating from inner wall of mature capsule (i.e., septa elastic). Seeds 2 (or fewer by abortion) per valve, discoid, covered with hygroscopic trichomes.

Twenty-two species are native in the Old World, primarily in tropical Africa; at least one species has become naturalized in the American tropics. *Phaulopsis* pertains to subfamily Acanthoideae, tribe Ruellieae.

Phaulopsis micrantha (Benth.) C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. 5:85. 1899, as "*Phaylopsis micrantha*." *Aetheilema micranthum* Benth. in W. Hooker, Niger Fl. 480. 1849, as "*Aetheilema micrantha*." TYPE.— SÃO TOMÉ AND PRÍNCIPE. São Tomé: without locality, *Don s.n.* (holotype: BM).

Phaylopsis obliqua T. Anders. ex Moore, J. Bot, n.s. 9:229. 1880. *Micranthus obliquus* (T. Anders. ex Moore) Kuntze, Rev. Gen. Pl. 2:493. 1891.
Micranthus hensii Lindau, Bot. Jahrb. Syst. 22:114. 1895.

Sprawling to erect annual to perennial herbs to 4 dm tall; young stems quadrate-sulcate, pubescent with ± retrorse eglandular trichomes 0.05–0.2 mm long and usually (especially distally) with an overstory of erect to flexuose eglandular and glandular trichomes to 1 mm long. Leaves mostly anisophyllous, petiolate, petioles to 32 mm long, blades ovate to broadly ovate, 3–81 mm long, 2–42 mm wide, 1.5–2.4 × longer than wide, acute to acuminate at apex, truncate-acute to acute and often oblique at base, margin entire to subsinuate, surfaces sparsely pubescent with antrorse eglan-

dular trichomes (e.g., older and larger leaves) or also pubescent with erect to flexuose glandular and eglandular trichomes to 1 mm long (e.g., younger and smaller leaves or bracts). Inflorescence often borne from near base of plant to apex, consisting of pedunculate loose unilateral spikes and/or solitary flowers and/or monochasia (sensu Manktelow 1996) borne in axils of leaves or reduced bractlike leaves, axillary flowers or monochasia sometimes forming a terminal spikelike inflorescence to 60 mm long (including peduncle); peduncles and rachises pubescent with erect to flexuose glandular and eglandular trichomes to 1.6 mm long. Bracts anisophyllous, foliose or greatly reduced in size; a deltate to oblate to rhombic bracteole (intracymal bract fide Manktelow 1996) also often subtending flower(s). Calyx 3–6 mm long, lobes heteromorphic, posterior lobe much larger than others, subfoliose. Corolla white, 4.2–5 mm long, externally sparsely pubescent with flexuose to retrorse eglandular trichomes 0.1–0.2 mm long, tube 2.8–3.8 mm long, expanded only near apex into a short throat, upper lip 0.5–1.3 mm long, 2-lobed, lobes 0.5–0.8 mm long, lower lip 1.3–1.8 mm long, 3-lobed, lobes 0.6–1 mm long. Stamens 4, inserted at 2 levels and anthers presented at 2 heights, included in corolla tube, longer (anterior) pair 1 mm long, shorter (posterior) pair 0.5 mm long; thecae 0.3 mm long, lacking basal appendages; pollen (fig. 7G–I) 3-porate, pores flanked by 2 ± curved liplike protrusions of exine, each mesocolpium with 5 (–6) pseudocolpi, interapertural surfaces foveolate-reticulate. Style pubescent with eglandular trichomes; stigma unequally 2-lobed, 0.3–0.4 mm long. Capsule 4–5 mm long, distally pubescent with erect mostly glandular trichomes 0.05–0.1 mm long. Seeds 1.1–1.3 mm long, 0.9–1.1 mm wide, surfaces and margin covered with hygroscopic trichomes to 0.5 mm long. Figure 4C–D.

Illustrations.— Heine (1966: 53, fig. 10, 1–10); Manktelow (1996:155, fig. 67, K–L).

Phenology.— Flowering and fruiting: April–July.

Distribution and habitats.— Central Africa (Angola, Central African Republic, Congo-Brazzaville, Congo-Kinshasa, Equatorial Guinea [Annobón], Gabon, São Tomé and Príncipe); plants occur in disturbed areas (e.g., plantations, roadsides) and secondary forest at elevations from sea level to 1900 m. In São Tomé and Príncipe plants occur only on São Tomé on moist banks in regions of montane moist to wet forest and in disturbed areas (e.g., plantations) at elevations from 40 to 600 (–1900?) m. This is the only species of Acanthaceae that occurs only on both São Tomé and Annobón among the major islands in the Gulf of Guinea.

Conservation.— Although known from several nations of tropical central Africa, this species is not known from many collections from São Tomé. However, it is somewhat weedy and probably more under-collected than truly rare on the island.

Local name.— "Fiá glavana" (*Espírito Santo 4653*).

Notes.— The structure of the inflorescence is particularly complex in *Phaulopsis*. Manktelow (1996) noted that this species has the smallest flowers in the genus. Based on a morphological phylogenetic study, Manktelow (1996) indicated that its relatives were three species in a derived clade of annuals: *P. verticillaris* (Nees) Manktelow from Comoros and Madagascar; *P. dorsiflora* (Retz.) Santapau from regions in the Indian Ocean (e.g., Réunion), southern Asia, and southeastern Asia; and *P. talbotii* S. Moore from the West Indies and northern South America (where possibly naturalized as a result of historical introduction) and northern tropical Africa.

Manktelow (1996) noted an elevation of 1900 m for the species from "Grand Pico, São Tomé." No specimens from that elevation have been seen.

Additional specimens examined.— **São Tomé**: ca. 2.5–3 km (air) SE of Ponta Figo toward Pico São Tomé, at and ca. 0.5 km from Resevoir Centrale Hydroélectrique, 00°19.050′N, 006°33.005′–33.013′E, *T. Daniel 11145* (CAS, K, MO, STPH); Santa Catarina, *J. Espírito Santo 4653* (LISC); Roça Rodia e Monte Café, *A. Moller 87 e 514* (COI, LISU); próx. ao Bate-pá, *A. Moller 330* (BR, COI); Roça Rio do Ouro, *A. Moller 558* (COI); Roça Uba Budo, *F. de Oliveira 264* (STPH).

Rhinacanthus Nees in Wallich, Pl. As. Rar. 3:76. 1832

TYPE.— *Rhinacanthus communis* Nees, nom. illeg. (= *Justicia nasuta* L., *Rhinacanthus nasutus* (L.) Kurz.).

Perennial herbs or shrubs with cystoliths. Leaves opposite, entire (sometimes undulate-crenate). Inflorescence of axillary or terminal dichasiate spikes, these sometimes forming panicles; dichasia 1–many-flowered; flowers subtended by 2 bracteoles. Calyx 5-lobed, lobes subequal in size. Corolla white, purple, or greenish, tube elongate, narrow, cylindric, usually conspicuously longer than limb, limb 2-labiate, upper lip internally rugulate, entire to 2-fid, lower lip 3-lobed, corolla lobes ascending-cochlear in bud. Stamens 2, exserted from mouth of corolla; anthers 2-thecous, thecae of a pair subequal to unequal in size, perpendicular to subparallel, unequally inserted to superposed (contiguous to separated), lower theca with or without a basal appendage; pollen 3-colporate, either 6-pseudocolpate or with apertures flanked on each side by one row of barely distinct to prominent ± circular insulae in a "trema" region; staminodes 0. Capsule stipitate, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic). Seeds 2 (or fewer by abortion) per valve, discoid.

Rhinacanthus is an Old World genus of about 25 species that occur in Africa, Madagascar, Socotra, and Asia. Phylogenetic studies based primarily on DNA sequence data place it in subfamily Acanthoideae, tribe Justicieae, subtribe Diclipterinae (McDade et al. 2000). Although the genus appears morphologically more similar to *Justicia* (e.g., rugula, pollen), these molecular studies suggest a closer relationship to *Dicliptera* and its relatives. African taxa were recently revised by Darbyshire and Harris (2006), who recognized 15 species from the continent.

Rhinacanthus virens (Nees) Milne-Redh. in Exell, Suppl. Cat. Vasc. Pl. S. Tome, 37. 1956. *Leptostachya virens* Nees in Alph. de Candolle, Prodr. 11:378. 1847. TYPE.— "Gaboon Coast," *Middleton s.n.* (holotype: K ex herb. Benth.).

Rhinacanthus dewevrei De Wild. & Th. Dur., Bull. Soc. Roy. Bot. Belgique 38:105. 1899.
Rhinacanthus subcaudatus C.B. Clarke, Fl. Trop. Afr. 5:225. 1900.

Perennial herbs to 1 m tall; young stems pubescent with antrorse eglandular trichomes 0.3–0.7 mm long, trichomes ± restricted to angles and thus generally in 4–6 lines. Leaves petiolate, petioles to 20 mm long, blades elliptic to ovate elliptic to lance-elliptic, 47–170 mm long, 17–55 mm wide, 2.6–4.9 × longer than wide, acute to acuminate at apex, acute to subattenuate at base, surfaces sparsely pubescent, margin entire, ciliate. Inflorescence of axillary panicles of few-flowered spicate axes, inflorescence branches subtended by foliose (generally smaller than leaves) or subulate (4–5.5 mm long, 0.4–0.6 mm wide) bracts, rachises pubescent with erect to antrorse and mostly eglandular (sometimes with a few subglandular) trichomes 0.05–0.3 mm long and often with an overstory of antrorse and mostly eglandular (sometimes with a few glandular) trichomes 0.3–0.5 mm long. Bracts subulate 3–7 mm long, 0.4–0.5 mm wide. Bracteoles subulate, 2.5–4 mm long. Flowers 1–2 at bracteal nodes or ± clustered near apex of inflorescence branches, sessile to subsessile (i.e., borne on pedicels to 1 mm long). Calyx 5-lobed, 5–6.5 mm long, lobes subulate, subequal in length, 4.2–5.5 mm long, abaxial surface pubescent with erect eglandular and glandular trichomes 0.05–0.2 mm long. Corolla white, 12–16 mm long, externally pubescent with flexuose eglandular trichomes, tube 9–12 mm long, upper lip 2–3.5 mm long, lower lip 3–4 mm long. Stamens 2.5–3 mm long; thecae 0.7–1 mm long, subequal in length, unequally inserted, subperpendicular to subparallel, lower theca with a basal appendage 0.1–0.2 mm long; pollen (fig. 7E–F) 3-aperturate, apertures (colpori) flanked on each side by one row of barely distinct to prominent ± circular insulae in a "trema" region, interapertural surfaces reticulate. Style 9.5 mm long, proxi-

mally pubescent with eglandular trichomes, distally glabrous; stigma 0.4 mm long. Capsule 12–16 mm long, pubescent with flexuose to retrorse eglandular trichomes. Seeds 1.8–2.6 mm long, 1.8–2 mm wide, surfaces and margin covered with apically rounded peglike tubercles to 0.05 mm long. Figure 4H–I.

Illustration.— Heine (1966:203, fig. 42).

Phenology.— Flowering and fruiting: December–April.

Distribution and habitats.— Tropical Africa (Cameroon, Central African, Republic, Congo-Kinshasa, Gabon, Ghana, Guinea, Ivory Coast, Liberia, Nigeria, São Tomé and Príncipe, Sierra Leone, Togo). In São Tomé and Príncipe, plants occur only on Príncipe in regions of moist to wet secondary montane forest at elevations from 190 to 350 m.

Conservation.— Although widely distributed in tropical western and central Africa, this species is known from relatively few collections on Príncipe. It is likely more under-collected than truly rare there.

Notes.— This species was listed as *R. dewevrei* by Exell (1944). This name and *R. subcaudatus* were subsequently treated as synonyms of *R. virens* (Heine 1963; Exell 1973). Plants from Príncipe were treated as *R. virens* var. *virens* by Heine (1963) and by Exell (1973). Plants from Príncipe conform to *R. virens* as treated by Darbyshire and Harris (2006).

Pollen of *R. virens* from Príncipe is somewhat intermediate between *Justicia* (presence of insulae in a "trema" region) and *Dicliptera* (3-colporate). Pollen from most species of *Rhinacanthus* has yet to be characterized.

Additional specimens examined.— **Príncipe**: vicinity of Santa Trindade (= Roça Pico Papagaio) at N slope of Pico Papagaio, between Esperança and São Joaquim (Oeste), 01°37.156′N, 007°23.540′E, *T. Daniel 11156* (CAS, K, MO, STPH); cultivated lands, *J. Espírito Santo 222* (COI); entre Rio Banzú-Pico João Dias Pai e João Dias Filho, *F. Oliveira 133/98* (BRLU, LISC, STPH); without locality, *F. Welwitsch 5204* (LISU); W side of Barriga Branca, ca. 3 km SSW of Maria Correia, *J. de Wilde et al. 377* (WAG).

Ruellia L., Sp. Pl. 634. 1753

Lectotype (designated by Britton and Brown, Ill. Fl. N. U.S., ed. 2, 3:241. 1913): *Ruellia tuberosa* L.

Perennial herbs, shrubs, or (rarely) trees with cystoliths. Leaves opposite, entire to sinuate to crenate to dentate. Inflorescence of reduced or expanded dichasia in axils of leaves or bracts, sometimes forming dichasiate spikes, thyrses, or panicles; dichasia 1-many flowered; flowers usually subtended by 2 bracteoles (these sometimes vestigial or absent), sometimes of two types: chasmogamous flowers generally large and showy, cleistogamous flowers budlike and commonly preceding or succeeding chasmogamous flowers. Calyx 5-lobed, lobes equal or unequal in size. Corolla of chasmogamous flowers blue, blue-purple, pink, red, white, or yellow, rarely blackish, usually lacking colored nectar guides, tube usually funnelform, expanded distally into a ± distinct throat (rarely saccate), limb 2-labiate (upper lip 2-lobed, lower lip 3-lobed) to subactinomorphic (subequally 5-lobed), corolla lobes contorted in bud. Stamens 4, included in corolla tube or exserted from mouth of corolla; anthers 2-thecous, thecae of a pair usually equal in size, parallel to subsagittate, equally inserted, lacking basal appendages; pollen 3-porate; staminodes 0–1. Capsule substipitate to stipitate, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic) or (rarely) with septa and attached retinacula separating from inner wall of mature capsule (i.e., septa elastic). Seeds (2–) 4–10 (or fewer by abortion) per valve, discoid, pubescent with hygroscopic trichomes (sometimes restricted to margin).

The generic boundaries of *Ruellia* have been debated for many years. In one broad sense it comprises approximately 250 species worldwide with species occurring primarily in the tropics

and subtropics. Some of the generic synonymy, primarily for New World taxa, has been reviewed by Daniel (1995) and Ezcurra (1993). The genus pertains to subfamily Acanthoideae, tribe Ruellieae.

Ruellia brevifolia (Pohl) Ezcurra, Darwiniana 29:278. 1989. *Stephanophysum brevifolium* Pohl, Pl. Bras. Icon. Descr. 2:84. 1831. **Type**.— BRAZIL. Rio de Janeiro: Rio de Janeiro, *Schott s.n.* (holotype: W).

Stephanophysum longifolium Pohl, Pl. Bras. Icon. Descr. 2:85. 1831. *Ruellia longifolia* (Pohl) Griseb., Abh. Koenigl. Ges. Wiss. Göttingen 24:260. 1879, non Richard (1872). *Ruellia graecizans* Backer, Brittonia 3:85, 87. 1938.

A complete synonymy of this species was provided by Ezcurra (1993).

Erect perennial herbs to 7 dm tall; young stems quadrate, sparsely puberulent with erect eglandular trichomes < 0.1 mm long (and with longer flexuose trichomes at nodes). Leaves petiolate, petioles to 25 mm long, blades ovate to elliptic, 65–135 mm long, 25–57 mm wide, 2.3–3.1 × longer than wide, acuminate at apex, attenuate at base, surfaces subglabrous to puberulent with cauline type trichomes, margin entire to subsinuate-crenate. Inflorescence of long-pedunculate dichasia from axils of leaves, peduncles to 115 mm long, puberulent like young stems; dichasia expanded, 3–many-flowered. Bracteoles subfoliose, 13–22 mm long, 1.5–4.5 mm wide, secondary bracteoles similar to bracteoles except smaller. Flowers pedicellate, pedicels 3–7 (–11) mm long. Calyx 7–11 mm long, lobes subulate, 5–9 mm long, subequal in length, abaxially puberulent with cauline type trichomes. Corolla red, 30–35 mm long, externally puberulent with eglandular and subglandular trichomes to 0.1 mm long, tube 25–30 mm long, expanded into a throat, narrow proximal portion 5–6 mm long, throat 20–24 mm long, 10–13 mm in diameter near midpoint, limb ± 2-labiate, upper lip 4–6 mm long, lobes 2.5–3.5 mm long, lower lip 5–8 mm long, lobes 4–6 mm long. Stamens 13–15 mm long, at least partially exserted from mouth of corolla but not extending beyond lips; thecae 1.7–1.9 mm long. Style 26 mm long, slightly exserted from mouth of corolla. Capsule stipitate, obovoid to clavate, 15–19 mm long, externally pubescent with glandular and eglandular trichomes < 0.1 mm long, stipe 4–5.5 mm long. Seeds 6 (or fewer by abortion) per valve, 2.7–3 mm long, 2–2.6 mm wide, surface smooth, margin covered with a ring of hygroscopic trichomes.

Illustrations.— Ezcurra (1993:803, fig. 7); Bosser and Heine (2000:15, pl. 4).

Phenology.— Flowering: August–April; fruiting: August–February.

Distribution and habitats.— Native to southern South America; plants are widely cultivated for ornament and sometimes naturalized in tropical regions (e.g., Mascarene Islands; Bosser and Heine 2000). In São Tomé and Príncipe, introduced plants have become naturalized only on São Tomé, where they occur in regions of second growth and in disturbed areas (e.g., cacao plantations, trailsides, roadsides) at elevations of 10–700 m.

Local names.— "Mato-baná" (*Espírito Santo 4163*), "pega-pega" (*Espírito Santo 4163*).

Notes.— This species was listed by Exell (1973) and Figueiredo (1996, 2002) as *Ruellia graecizans*, a synonym by which the species has been commonly known in the horticultural trade. It was undoubtedly introduced as an ornamental to São Tomé where it has become naturalized in disturbed habitats on many parts of the island.

Additional specimens examined.— **São Tomé**: along road (EN-1) from São Tomé to Santa Catarina between Guadalupe and Conde at base of hill at Muquinqui, 00°22.648′N, 006°38.630′E, *T. Daniel 11121* (CAS, MO, STPH); Rio do Ouro, *J. Espírito Santo 3865* (COI, LISC), *4163* (LISC); Morro Muquinqui, *E. Figueiredo & P. Arriegas 30* (LISC); Santo Amaro, *N. Garcia 45/Nu* (COI); Muquinqui, 00°22.85′N,

006°39.10′E, *G. Joffroy 179* (BRLU, LISC, STPH); Monte Café, 00°18′N, 006°38′E, *C. de Matos & K. van Essche 7668* (BRLU, LISC, STPH); Guadalupe, *T. Monod 11894* (COI); Desejada, *F. Oliveira 174* (STPH); Zona Bindá–J. Sousa, 00°13′N, 006°28′E, *F. de Oliveira 333* (STPH); Diana, 00°19′45″N, 006°41′00″E, *T. Stévart & F. de Oliveira 19* (BRLU, STPH).

Stenandriopsis S. Moore, J. Bot. 44:153. 1906

Type.— *Stenandriopsis thompsonii* S. Moore.

Perennial herbs or shrubs lacking cystoliths. Leaves opposite or in whorls of 4, margin entire to subcrenate to dentate. Inflorescence of axillary or terminal dichasiate spikes (rarely reduced to 1 or 2 dichasia); dichasia 1-flowered; flowers subtended by 2 bracteoles. Calyx 5-lobed, lobes subequal in size (one ± larger than others), conspicuously thickened at base. Corolla white or blue or purple or pinkish, sometimes with colored spots on limb or throat, tube cylindric or ± expanded distally into a throat, limb 2-labiate (upper lip 2-lobed, lower lip 3-lobed) to subactinomorphic (subequally 5-lobed), corolla lobes ascending-cochlear in bud. Stamens 4, included in corolla tube; anthers 1-thecous, pubescent, lacking basal appendages; pollen 3(–6)-colpate; staminode 0–1. Capsule estipitate, linear-ellipsoid to obovoid, retinacula present and remaining attached to inner wall of mature capsule (i.e., septa inelastic). Seeds 2 (or fewer by abortion) per valve, discoid to irregularly triangular to subsquare in outline.

Twenty species from tropical Africa (10 species) and Madagascar (10 species). Vollesen (1992) equated the Old World genus *Stenandriopsis* with the New World *Stenandrium*. Indeed, there are no known morphological differences between species from the two regions. Phylogenetic data based on molecular sequences (McDade et al. 2005) suggest that they should be treated as distinct. Both genera pertain to subfamily Acanthoideae, tribe Acantheae (McDade et al. 2005).

Stenandriopsis thomensis (Milne-Redh.) Heine, Fl. Gabon 13:99. 1966. *Crossandra thomensis* Milne-Redh., Bull. Misc. Inf. Kew 1935:280. 1935. *Stenandrium thomensis* (Milne-Redh.) Vollesen, Kew Bull. 47:187. 1992. **Type.**— SÃO TOMÉ AND PRÍNCIPE. São Tomé: Angolares, Rio Salgado, 50 m, Jan 1886, *F. Quintas 1089* (holotype: COI! isotype: BM).

Perennial herbs to 2.5 dm long or tall, proximal portions of stems creeping and rooting, distal portions of stems ascending; young stems quadrate-sulcate, densely pubescent with flexuose-ascending multi-septate purplish trichomes to 2 mm long. Leaves opposite, petiolate, petioles to 20 mm long, blades discolorous (paler abaxially), obovate to pandurate to elliptic, 25–95 mm long, 15–55 mm wide, 1.4–2.7 × longer than wide, acute to subacute at apex, cordate to subcordate at base, margin entire to sinuate, surfaces pubescent with eglandular trichomes. Inflorescence of terminal subsessile to pedunculate dichasiate spikes, peduncles 3–10 mm long; dichasia 1-flowered, opposite to subopposite to alternate. Bracts ovate-elliptic to elliptic, subaristate at apex, abaxial surface puberulent with trichomes to 0.05 mm long, margin dentate in distal half, teeth 1–3 per side (proximalmost bracts rarely entire to subentire). Bracteoles lanceolate, 9–13 mm long, abaxial surface pubescent like bracts. Flowers sessile. Calyx 14–18 mm long, lobes lanceolate, subequal in size, 2 lateral lobes smallest, abaxial surface of lobes pubescent like bracts. Corolla blue, lilac, or purplish, 32–40 mm long, externally glabrous, tube 20–26 mm long, limb 20–29 mm in diameter, upper lip with lobes 12 mm long, 5 mm wide, lower lip with lobes 15 mm long, 12 mm wide. Stamens 4 mm long; thecae 2.4–3 mm long; pollen (based on Furness 1993) 3-colpate, interapertural surfaces reticulate. Style 18–20 mm long, sparsely pubescent with eglandular trichomes. Capsule 12–15 mm long, glabrous. Seeds 2.7–3.5 mm long, 1.8–3 mm wide, densely tuberculate with rounded, peglike tubercles to 0.2 mm long.

Illustration.— Vollesen (1992:180, fig. 1, A–H).

Phenology.— Flowering: January–October; fruiting: January, April.

Distribution and habitats.— Restricted to the Gulf of Guinea region in tropical western Africa (Cameroon, Nigeria, São Tomé and Príncipe). In São Tomé and Príncipe plants occur in lowland to lower montane moist to wet primary and secondary forests at elevations of 50–800 m.

Conservation.— This is a somewhat rare species of limited occurrence in São Tomé and Príncipe. However, it occurs on both islands (as well as on the African mainland), and at least part of its range is inside the protected Parque Natural Obô.

Notes.— Vollesen (1992) noted that this distinctive species was known from only four collections from São Tomé and Cameroon. Collecting activities since his account have resulted in additional specimens and distribution records, including one from Príncipe and another from Nigeria. In addition to the collections cited below, the species was reported to have been collected on São Tomé at Morro Vilela (00°17′N, 006°32–33′E, 1167–1338 m, *de Oliveira 1281* and *1533* at BRLU, not seen). Although the species shows similarities with several species in eastern Africa, Vollesen (1992) noted that it was more closely related to the tropical western and central African species *S. guineense* (Nees) Benoist and *S. talbotii* (S. Moore) Heine.

Additional specimens examined.— **Príncipe**: Pico Papagaio (zona ecológica), 01°36′45″N, 007°23′30″E, *F. de Oliveira 547* (BRLU, STPH). **São Tomé**: Ribeira Peixe, Dependência de Monte Carmo, *J. Espírito Santo 3883* (COI, LISC); Ribeira Peixe, S do Cabumbé, *J. Espírito Santo 3903* (LISC); San Miguel, Monte Verde, 00°09′N, 006°30′E, *J. Lejoly 95/97* (BRLU, LISC, STPH); Rio Xufexufe, 00°10′N, 006°31′E, *C. de Matos & K. van Essche 7253* (BRLU, LISC, STPH); São Miguel, 00°08′30″N, 006°29′50″E, *C. de Matos & K. van Essche 7653* (BRLU, LISC, STPH); descent towards the valley of R. Ió Grande (00°10′N, 006°36′E), *F. de Oliveira 1365* (BRLU), *1368* (BRLU); Parc National d'Obo, Rio Xuf Xuf, 00°08′30″N, 006°30′15″E, *T. Stévart & F. de Oliveira 154* (BRLU).

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Appendix 1

Native species of Acanthaceae, including **endemics**, on each of the major islands in the Gulf of Guinea. Bioko and Annobón (Pagalu) together form the Insular Region of Equatorial Guinea. Acanthaceae occurring on Bioko are based on Exell (1973) with updated nomenclature from Lebrun and Stork (1997). *Justicia mannii*, putatively endemic to Bioko, requires further study to determine its status.

Bioko (46): *Acanthopale decempedalis* C.B. Cl., *A.* sp., *Acanthus montanus*, *Afrofittonia silvestris* Lindau, *Asystasia gangetica*, *A. lindaviana* Hutch. & Dalz. (= *Filetia africana* Lindau), *A. macrophylla* (T. Anders.) Lindau, *A. vogeliana* Benth., *Avicennia germinans*, *Brachystephanus longiflorus* Lindau, *Brillantaisia lamium*, *B. madagascariensis* Lindau, *B. owariensis*, *B. vogeliana*, *Crossandrella dusenii* (Lindau) C.B. Cl., *Dicliptera laxata* C.B. Cl., *Dischistocalyx thunbergiiflorus* (T. Anders.) Benth. ex C.B. Cl., *Elytraria marginata*, *Hypoestes aristata* (Vahl) Soland. ex Roem. & Schult., *H. triflora* (Forssk.) Roem. & Schult., *Isoglossa glandulifera* Lindau, *I.* sp., *Justicia baronii* V.A.W. Graham (= *Adhatoda robusta* C.B. Cl.), *J. biokoensis* V.A.W. Graham (= *Adhatoda maculata* C.B. Cl.), *J. extensa* T. Anders., *J. insularis* T. Anders., *J. laxa* T. Anders., ***J. mannii*** T. Anders. (possibly equivalent to *J. orbicularis*, excluded as a possible mixture by Lebrun and Stork (1997)), *J. orbicularis* (Lindau) V.A.W. Graham (= *Adhatoda orbicularis* (Lindau) C.B. Cl.), *J. preussii* (Lindau) C.B. Cl., *J. tenella*, *J. tristis* (Nees) T. Anders. (= *Adhatoda tristis* Nees), *Mendoncia gilgiana* (Lindau) Benoist, *Mimulopsis solmsii* Schweinf., *Nelsonia smithii*, *Oreacanthus mannii* Benth., *Phaulopsis ciliata* (Willd.) Hepper (= *P. falcisepala* C.B. Cl.), *Pseuderanthemum ludovicianum* (Büttn.) Lindau, *P. tunicatum* (Afz.) Milne-Redh., *Ruellia primuloides* (J. Anders. ex Benth.) Heine, *Rungia paxiana* (Lindau) C.B. Cl., *Schaueria populifolia* C.B. Cl., *Sclerochiton preussii* (Lindau) C.B. Cl., *Stenandriopsis guineensis* (Nees) Benoist, *Thunbergia vogeliana* Benth., *Whitfieldia elongata* (P. Beauv.) De Wild. & Th. Dur.

São Tomé (14): *Asystasia gangetica*, *Avicennia germinans*, ***Brachystephanus occidentalis***, *Brillantasia lamium*, *B. owariensis*, *B. vogeliana*, *Dicliptera verticillata*, *Elytraria marginata*, ***Heteradelphia paulowilhelmia***, *Justicia tenella*, ***J. thomensis***, *Nelsonia smithii*, *Phaulopsis micrantha*, *Stenandriopsis thomensis*.

Príncipe (9): *Acanthus montanus*, *Asystasia gangetica*, *Brillantaisia lamium*, *Dicliptera verticillata*, *Elytraria marginata*, *Justicia tenella*, *Nelsonia canescens*, *Rhinacanthus virens*, *Stenandriopsis thomensis*.

Annobón (3): *Avicennia germinans*, *Dicliptera verticillata*, *Phaulopsis micrantha*.

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Phylogenetic Relationships among Species in the Sphaerodactylid Lizard Genus *Pristurus*

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The gecko genus *Pristurus* Rüppell, 1835 (Squamata: Sphaerodactylidae) contains at least 20 currently recognized species. One species occurs in Mauritania and the remaining species are found in northeast Africa, the Horn of Africa, the Arabian Peninsula, the Socotra Archipelago, Jordan, and coastal Iran (Arnold 2006).

Previous phylogenetic studies used morphological and ecological characters of the genus (Arnold 1977, 1986a, 1986b, 1990, 1993, 2009). Here we present a phylogeny based on molecular markers. Although only 11 described species are included in our data set, we have representatives from each of the species groups proposed by Arnold (2009). Our geographic coverage includes the Horn of Africa (four populations), Yemen mainland (three populations), Socotra Island (four populations), Oman (seven populations), and Sharjah (one population; Fig. 1).

Arnold (2009) recognized the subgenus *Spatulura* Gray, 1863 for a group of nine derived *Pristurus* species with numerous morphological synapomorphies. This study includes *P. carteri* (Gray, 1863), *P. minimus* Arnold,

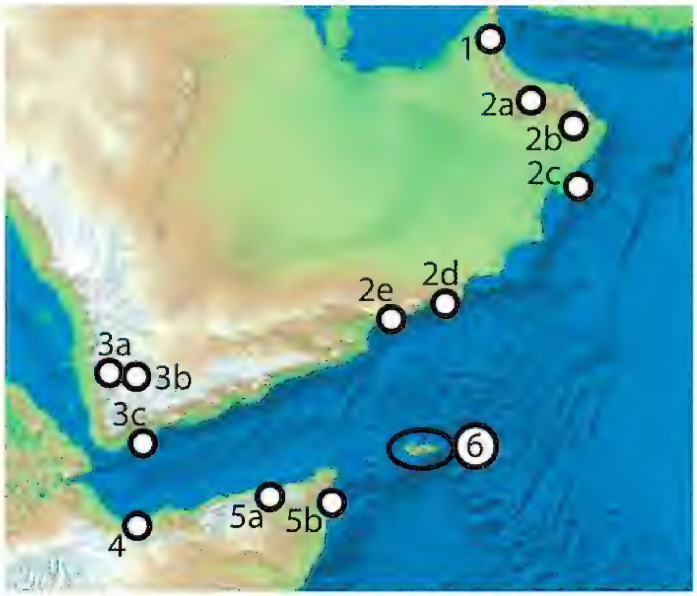

FIGURE 1. Map of the Horn of Africa, Socotra Island, and the southeastern portion of the Arabian Peninsula showing location of *Pristurus* samples used in this study. 1- Sharjah, (*Pristurus sp. 2*); 2a- Oman (*Pristurus celerrimus*; *Pristurus* sp. 2); 2b- Oman (*Pristurus minimus*); 2c- Oman, Masirah Island (*Pristurus carteri*); 2d- Oman (*Pristurus carteri*); 2e- Oman (*Pristurus* sp. 1); 3a- Yemen (*Pristurus* sp. 1); 3b- Yemen (*Pristurus* sp. 1); 3c- Yemen (*Pristurus rupestris*); 4- Somaliland (*Pristurus somalicus*); 5a- Somalia (*Pristurus flavipunctatus*; *Pristurus somalicus*); 5b- Somalia (*Pristurus crucifer*); 6- Socotra Island.

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1977, *P. crucifer* (Valenciennes, 1861), and *P. somalicus* Parker, 1932, from the subgenus *Spatulura*. The remaining species are "a less derived paraphyletic unit within which formal names are not applied" (Arnold 2009). Six of these, including the Oman endemic *P. celerrimus* Arnold, 1977 and the five endemic Socotra Archipelago species are called "the more primitive species of *Pristurus*" (Arnold 2009). This study includes *P. celerrimus, P. sokotranus* Parker, 1938, *P. insignus* Blanford, 1881, *P. guichardi* Arnold, 1986, and *P. abdelkuri* Arnold, 1986. The remaining five species are called "the *P. flavipunctatus* assemblage" (Arnold 2009). This study includes *P. flavipunctatus* Rüppell, 1835, and P. *rupestris* Blanford, 1874 from the "*P. flavipunctatus* assemblage."

Materials and Methods

Our study includes DNA sequence data from 19 museum vouchers at the California Academy of Sciences, San Francisco, California, USA (CAS) and the Museum of Vertebrate Zoology, University of California, Berkeley, California, USA (MVZ). Detailed locality information is available from these institutions. Species names, general localities, museum numbers and GenBank numbers are presented in Table 1. Species names for the populations sampled were selected using the following criteria: (1) specimens that match the original morphological descriptions and were collected from localities given for holotype or paratypes (*P. celerrimus*– CAS 225355; *P. carteri*– MVZ 241393; *P. guichardi*– MVZ 236529; *P. insignus*– MVZ 236530); (2) specimens identified using keys in Arnold (1986) and collected from localities within the known range of a given species (*P. flavipunctatus*– MVZ 242767; *P. rupestris*– MVZ 236545); (3) expert identification of specimens from Somalia (*P. crucifer*– MVZ 242784; *P. somalicus*– MVZ 242788, E. Nicholas Arnold, British Museum of Natural History, pers. com., 2006); (4) specimen from a locality reported in the literature (Wranik et al. 2004) and identified using original description (*P. abdelkuri*– MVZ 236525).

Table 1. Samples of *Pristurus* sequenced in this study.

Species	General Locality	Museum Number	Genbank Number RAG1	Genbank Number ND2
P. abdelkuri	Socotra Island	MVZ 236525	GU256883	GU271137
P. carteri	Dhofar, Oman	MVZ 242761	GU256885	GU271139
P. carteri	Masirah Is., Oman	CAS 225346	GU256884	—
P. carteri	Masirah Is., Oman	MVZ 241393	—	GU271138
P. celerrimus	Nothern Oman	CAS 225335	GU256886	GU271140
P. crucifer	Puntland, Somalia	MVZ 242784	GU256887	GU271141
P. flavipunctatus	Puntland, Somalia	MVZ 242767	GU256889	GU271143
P. guichardi	Socotra Island	MVZ 236529	GU256890	GU271144
P. insignus	Socotra Island	MVZ 236530	GU256891	GU271145
P. minimus	Oman	CAS 225390	GU256892	—
P. rupestris	Yemen	MVZ 236545	GU256888	GU271142
P. sokotranus	Socotra Island	MVZ 236553	GU256895	GU271149
P. somalicus	Puntland, Somalia	MVZ 242788	GU256897	GU271150
P. somalicus	Somaliland	CAS 225515	GU256896	—
Pristurus sp. 1	Marib, Yemen	MVZ 236547	—	GU271146
Pristurus sp. 1	Marib, Yemen	MVZ 236551	GU256893	GU271147
Pristurus sp. 1	Dhofar Oman	MVZ 242770	GU256894	GU271148
Pristurus sp. 2	Sharjah, UAE	CAS (pending)	—	GU271151
Pristurus sp. 2	Northern Oman	MVZ 241398	GU256898	GU271152

Total genomic DNA was extracted from liver or muscle tissue using PureGene Animal Tissue DNA Isolation Protocol (Gentra Systems, Inc.). A fragment of mitochondrial DNA that encodes the NADH dehydrogenase subunit 2 (ND2) gene and flanking tRNAs was amplified by the polymerase chain reaction (PCR; 94°C 45s, 48°C 30s, 72°C 1 min) for 35 cycles using the primer L4437 (Macey et al. 1997) and H5934 (Macey et al. 1997) or H-Alaliz (5'-AAAGTGTTTGAGTTG-CATTCA-3'). A fragment of nuclear DNA that encodes part of the recombination activating protein 1 (RAG-1) gene was amplified by PCR (94°C 45s, 55°C 30s, 72°C 1 min) for 35 cycles using the primers L-RAG1b and H-RAG1b (Kearney and Stuart 2004). PCR products were electrophoresed in a 1% low melt agarose TALE gel stained with ethidium bromide and visualized under ultraviolet light. The bands containing DNA were excised and agarose was digested from bands using GELase (Epicentre Technologies). PCR products were sequenced in both directions by direct double strand cycle sequencing using the amplifying primers and Big Dye version 3 chemistry (Perkin Elmer). The internal primers L-snRAG1 and H-snRAG1 (Kearney and Stuart, 2004) were also used in the RAG-1 sequencing reactions. Cycle sequencing products were precipitated with ethanol, 3 M sodium acetate, and 125 mM EDTA, and sequenced with a Prism 3100 Genetic Analyzer (ABI) or 3730 DNA Analyzer (ABI). Sequences were edited using Sequencher v. 4.1 (Genecodes).

Results and Discussion

A 1,457 bp fragment of mtDNA (ND2 and 5 tRNAs) was obtained from 16 populations representing 10 described species and 6 populations in two different clades for which names are not available (Fig. 2). A 1,381 bp fragment of nuDNA RAG1 was obtained from 16 populations representing 11 described species and 2 unnamed clades (Fig. 3). Maximum likelihood trees for each gene separately were estimated using GARLI (Zwickl, 2006), with parameter and branch length estimated simultaneously. We used nonparametric bootstraps (500 pseudoreplicates) to assess node support in resulting topologies. The Akaike Information Criterion (AIC) in ModelTest 3.06 (Posada and Crandall, 1998) was used to find the model of evolution that best fit the data for subsequent maximum-likelihood (ML) analysis. In the ML analysis, the GTR + Γ + I model was used.

In both the mitochondrial and nuclear trees, *Pristurus celerrimus* from Oman (lineage A) is sister to all other *Pristurus* (Figs. 2, 3). Three of the four species from Socotra Island, *P. insignus, P. sokotranus,* and *P. guichardi* (lineage B) form a monophyletic group that is sister to the remaining populations from the Arabian Peninsula, the Horn of Africa, and to *P. abdelkuri,* a Socotra Archipelago endemic.

The remaining populations contain three well-supported lineages (lineages C–E). Lineage C is represented by a specimen from the Dhofar region of Oman and a specimen from the Marib region of Yemen. These samples are catalogued as *Pristurus rupestris,* but may represent an undescribed form. Lineage D consists of *P. abdelkuri, P. rupestris* from the Aden region of southwestern Yemen, *P. flavipunctatus* from Somalia, and an apparent undescribed species from the Jebel Akhdar of northern Oman. Because it includes *P. flavipunctatus,* this lineage is the equivalent of the "*P. flavipunctatus* assemblage" of Arnold (2009). Lineage E includes four species within the subgenus *Spatulura.* Two species, *P. somalicus* and *P. crucifer,* are from the Horn of Africa and two species, *P. carteri* and *P. minimus*, are from Oman (Fig. 1).

Gamble et al. (2008) resurrected the family name Sphaerodactylidae and included 11 Old World and New World genera including *Pristurus* and *Teratoscincus,* the outgroup in this study. Our mitochondrial and nuclear DNA data generally support the relationships proposed by Arnold (2009) based on external features, osteology, myology and behavioral characters. Our lineage D

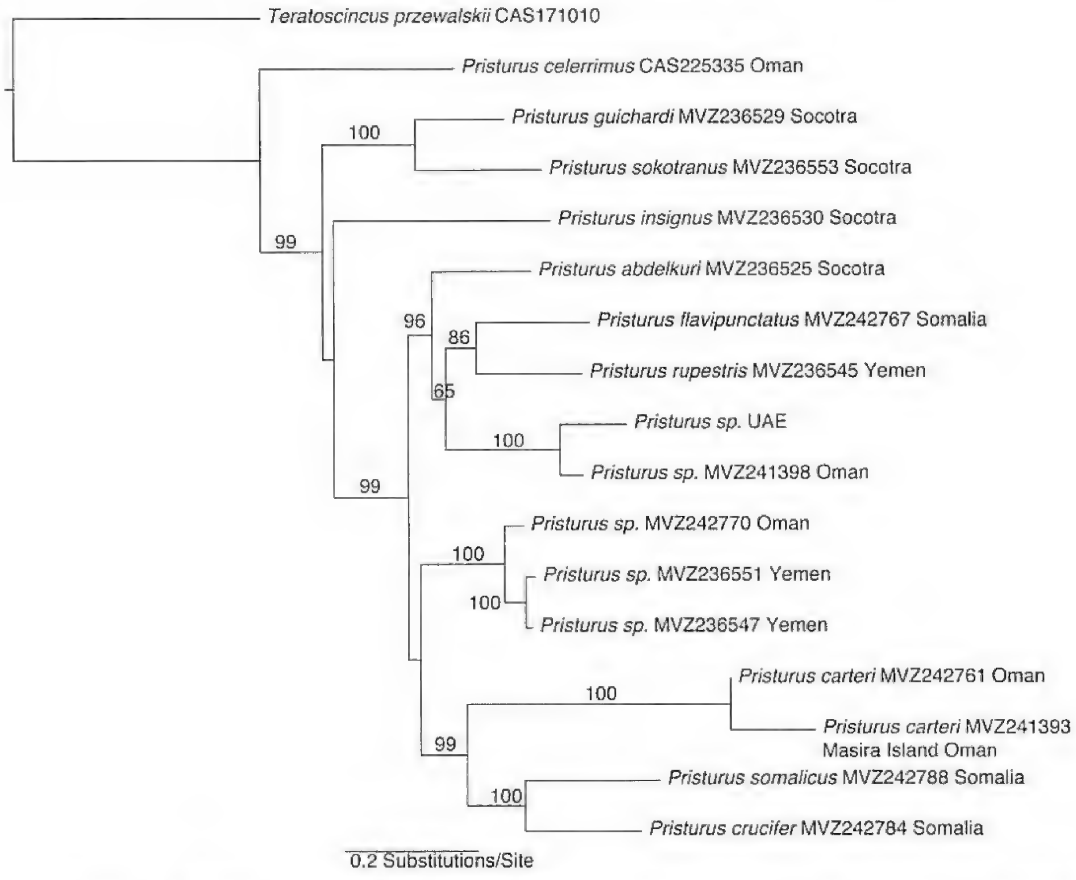

FIGURE 2. Maximum Likelihood phylogenetic hypothesis based on 1,457 aligned bases of mitochondrial ND2 and adjacent tRNA genes. Bootstrap support values over 50% (500 replicates) are indicated above the nodes.

includes *P. abdelkuri* along with *P. rupestris*, *P. flavipunctatus* and an undescribed form from northern Oman. This arrangement moves *P. abdelkuri* out of "the more primitive species" and into the "*P. flavipunctatus* assemblage" of Arnold (2009). *Pristurus abdelkuri* is found throughout Abd-el-Kuri Island, but Wranik et al. (2004) hypothesized that it was recently introduced to coastal Socotra around the town of Hadibou where they have been observed on rocks of the Hadibou littoral (Schätti and Desvoignes 1999). The specimen used in the study was collected at Hadibou.

The large ND2 mtDNA sequence divergences among the named species and the unnamed clades used in this study suggest that *Pristurus* is an extremely old lizard genus (Table 2). Macey et al. (2005), using dated geologic vicariant events, estimated sequence rates of divergence per million years for five species of the sphaerodactylid genus *Teratoscincus*. These rates ranged from 0.82 % per MY to 1.7% per MY. Two major geologic events, the formation of the Red Sea, which split the African and Arabian populations, and the separation of the Socotra Archipelago from the Arabian Peninsula have contributed to the speciation of *Pristurus*. Three Socotra endemics, *P. guchardi, P. insignus* and *P. sokotranus* (lineage B) have percent sequence differences to African and Arabian species that range from 27-41% (Table 2). Socotra is part of a limestone massif that separated from the Dhofar Mountains of southern Oman due to rifting in the Gulf of Aden and the Red Sea. This separation is thought to have occurred 34-41 MYBP (Macey et al. 2008) and the

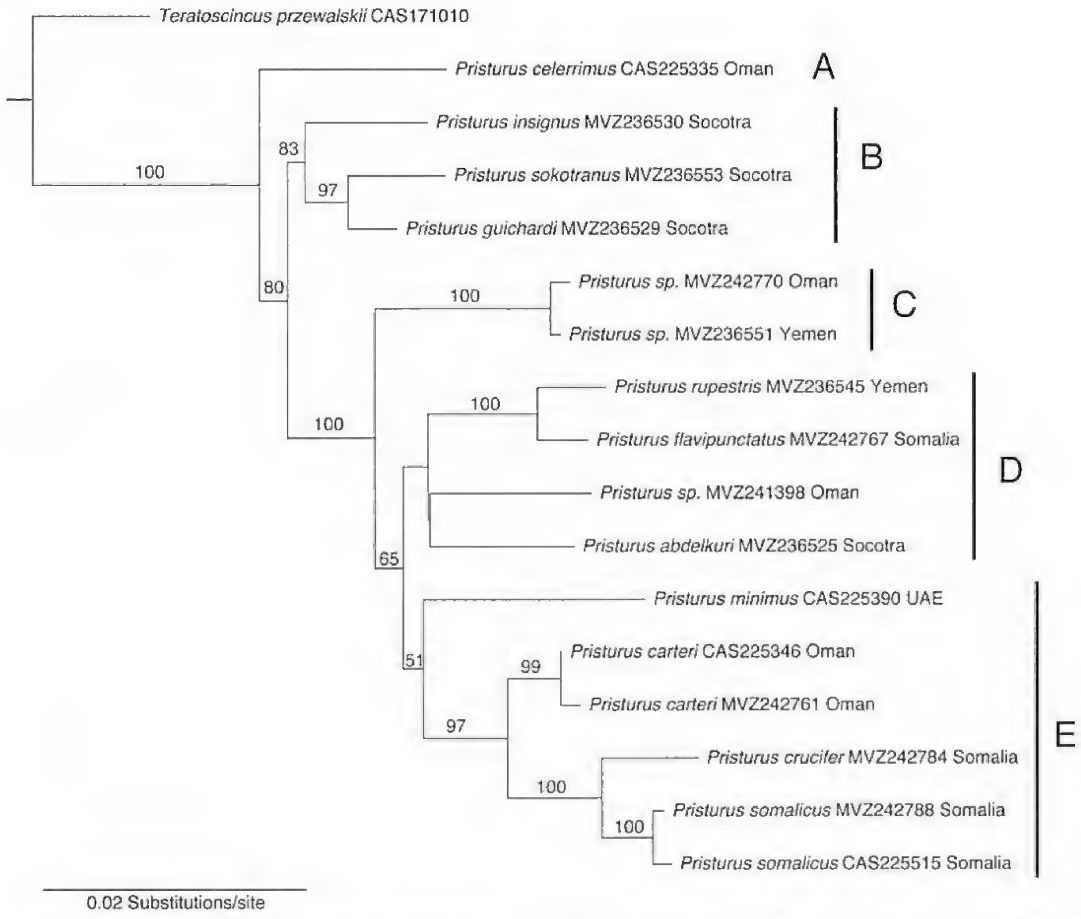

FIGURE 3. Maximum Likelihood phylogenetic hypothesis based on 1,381 bases of the nuclear RAG1 gene. Bootstrap support values over 50% (500 replicates) are indicated above the nodes. Five clades of interest (A-E) are indicated on the right.

observed sequence differences are concordant with the separation of Socotra from Arabia.

The fourth Socotra Archipelago species included in this study, *Pristurus abdelkuri,* belongs to lineage D, a clade that includes both Arabian Peninsula populations (*P. rupestris* from the Aden region of Yemen; *P.* sp. from northern Oman) and *P. flavipunctatus* from Somalia. *Pristurus abdelkuri* shows a 20-22% mt sequence divergence from other *Pristurus* in lineage D. The fact that *P. abdelkuri* shows lower sequence divergence from mainland forms than other Socotra endemics may indicate dispersal to Abd-el-Kuri Island after the separation of the Socotra Archipelago from Arabia.

Three species of *Pristurus, P. rupestris*, *P. crucifer*, and *P. flavipunctatus*, occur in both Africa and Arabia. At least one of these, *Pristurus rupestris*, is a species complex (E.N. Arnold, pers. com.). Unfortunately our data set does not include samples from both sides of the Red Sea-Gulf of Aden for any of the three. Samples from two species are included. *Pristurus flavipunctatus* (Somalia) and *P. rupestris* (Yemen) are both members of the *P. flavipunctatus* assemblage (Arnold 2009) and have an ND2 sequence divergence of 21%. *Pristurus somalicus* and *P. crucifer* (Somalia) and *P. carteri* (Oman) belong to the subgenus *Spatulura.* Sequence divergences between the Oman and

TABLE 2. Pairwise mtDNA sequence divergences among species of *Pristurus*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 *Pristurus abdelkuri* MVZ236525 Socotra	–																
2 *Pristurus carteri* MVZ241393 Masira Island Oman	0.388	–															
3 *Pristurus carteri* MVZ242761 Oman	0.283	0.115	–														
4 *Pristurus celerrimus* CAS225335 Oman	0.278	0.424	0.342	–													
5 *Pristurus crucifer* MVZ242784 Somalia	0.263	0.358	0.317	0.314	–												
6 *Pristurus rupestris* MVZ236545 Yemen	0.214	0.362	0.310	0.304	0.270	–											
7 *Pristurus flavipunctatus* MVZ242767 Somalia	0.203	0.352	0.273	0.293	0.277	0.209	–										
8 *Pristurus guichardi* MVZ236529 Socotra	0.283	0.412	0.346	0.303	0.314	0.275	0.297	–									
9 *Pristurus insignus* MVZ236530 Socotra	0.276	0.410	0.300	0.284	0.323	0.286	0.286	0.285	–								
10 *Pristurus* sp MVZ236547 Yemen	0.221	0.369	0.316	0.280	0.259	0.228	0.240	0.270	0.288	–							
11 *Pristurus* sp MVZ236551 Yemen	0.219	0.365	0.325	0.280	0.255	0.240	0.246	0.274	0.295	0.024	–						
12 *Pristurus* sp MVZ242770 Oman	0.196	0.379	0.272	0.266	0.269	0.242	0.227	0.271	0.267	0.069	0.072	–					
13 *Pristurus sokotranus* MVZ236553 Socotra	0.294	0.404	0.355	0.323	0.325	0.268	0.296	0.208	0.307	0.281	0.286	0.276	–				
14 *Pristurus somalicus* MVZ242788 Somalia	0.255	0.360	0.269	0.302	0.228	0.278	0.265	0.323	0.293	0.260	0.264	0.240	0.336	–			
15 *Pristurus* sp WB UAE	0.218	0.379	0.290	0.306	0.289	0.234	0.233	0.293	0.281	0.246	0.253	0.235	0.300	0.275	–		
16 *Pristurus* sp MVZ241398 Oman	0.208	0.387	0.289	0.291	0.287	0.232	0.207	0.285	0.279	0.236	0.242	0.217	0.290	0.269	0.100	–	
17 *Tetratoscincus przewalskii* CAS171010	0.354	0.444	0.366	0.331	0.370	0.364	0.348	0.359	0.343	0.362	0.360	0.340	0.377	0.359	0.360	0.351	–

Somalia samples range from 27–36%. The two species within Somalia are 23 % divergent (Table 2).

Our data for Africa and Arabia are not complete enough to support either dispersal or vicariant models. Both have certainly contributed to the present distribution of the genus. Future studies should attempt more detailed sampling of *Pristurus* from both Africa and Arabia. Our findings suggest that cryptic species are present in Arabia. Additional fieldwork is needed in Somalia and Somaliland where modern collections are limited and new forms are likely to be found. It is essential to obtain and compare samples of *P. rupestris*, *P. crucifer*, and *P. flavipunctatus* from both sides of the Red Sea. This small geographic area is ideal to test the effects of Oligocene rifting, Miocene land bridges, and almost certain dispersal events across the narrow Red Sea.

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Eviota randalli, a New Gobiid Fish from Oceania

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The Oceania populations of *Eviota pseudostigma* are recognized as a distinct species, *E. randalli*, from those in the Indian Ocean. *Eviota randalli* differs from *E. pseudostigma* in having more pectoral-fin rays but fewer of them branched and three rather than four subcutaneous body bars. Specimens from Palau remain as *incertae sedis*.

When Lachner and Karnella (1980) described *Eviota pseudostigma*, they noted differences between their specimens from the Indian Ocean and those from Oceania (the Society Islands [Tahiti] and the Samoa Islands [Tutuila]), restricting their type material to specimens from the Indian Ocean. They suggested that the widely separated populations may represent distinct species, but because they only had four specimens from Oceania they did not describe them as a separate species. Intensive collecting at Fiji resulted in ten specimens that were initially identified as *E. pseudostigma*, and R. Winterbottom provided three more specimens from Moorea. The differences observed by Lachner and Karnella were confirmed and the specimens from Oceania are here described as *E. randalli*.

Materials and Methods

Counts and measurements, descriptions of fin morphology and the laterosensory pore/neuromast patterns follow Lachner and Karnella (1980). Measurements were made to the nearest 0.1 mm using dial calipers and an ocular micrometer, and are presented as percentage of Standard Length (SL). Cyanine Blue 5R (acid blue 113) stain was used to make features more obvious (Akihito et al. 1993; Saruwatari et al. 1997; Nakabo 2002). Values for the holotype are given first, followed by the range in parentheses for all types, and by the mean where appropriate. Pectoral-fin ray counts in Table 1 combine those from Lachner and Karnella (1980) with those taken in this study. Institutional abbreviations are as listed in Leviton et al. (1985).

Species Description

***Eviota randalli* Greenfield, sp. nov.**
Figures 1–2.

Material Examined.—Holotype: CAS 228572, 16.8 mm SL, female, Fiji, Cobia Island, outside barrier reef, spur and groove, 16°27.333′S, 179°40.250′W, 12–17 m, rotenone, field number G03-55, D.W. Greenfield, T.A. Greenfield, R. Langston, J. Pilipoff, 22 May 2003. Paratypes: CAS 228573, 18.3 mm SL, male, Fiji, N. Lau Group, Duff Reef, barrier reef, N.W. side, coral rock on top of reef, 16°50.390′S,

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179°56.743′W, 0–1.8 m, rotenone, field number G03-36, D.W. Greenfield, K. Longenecker and R. Langston, 11 January 2003; CAS 228574, 17.6 mm SL, male, Fiji, N. Lau Group, Kanacea Island, N. side at Copra Plantation, barrier reef, crack in reef, 17°14.890′S, 179°08.475′W, 3.4–8.5 m, rotenone, field number G03-13, D.W. Greenfield, K. Longenecker, R. Langston, and B. K. Mataitini, 5 January 2003; CAS 219785, 16.8 mm SL male, 17.5 mm SL female, Fiji, Viti Levu, barrier reef off Suva, main channel, spur and groove, 18°′08′90″S, 178°23′91″E, 4.7–8.0 m, rotenone, field number G99-19, D.W. Greenfield, K. Longenecker and K. Cole, 31 May 1999. BPBM 41001, 17.1 mm SL, female, Fiji, N. Lau Group, Mago Island, N.W. side, cave in wall of fringing reef, 17°25.460′S, 179°10.085′W, 9.2 m, rotenone, field number G03-03, D.W. Greenfield, K.Longenecker, R. Langston, and B. K. Mataitini, 2 January 2003; USNM 396995, 16.6 mm SL, female, taken with BPBM 41001; ROM 84966 , 15.1 mm SL, male, Fiji, Vanua Levu, N. shore, outside Great Sea Reef, W of Kia Island, reef front, 16°13.730′S, 179°01.733′E, 4.3–10.8 m, rotenone, field number G02-125, D.W. Greenfield, K. Longenecker, R. Langston, and B. K. Mataitini, 31 March 2002; CAS 228575, 14.4 mm SL, male, 13.1 mm SL female, taken with ROM 84966; ROM 60894, male, 16.8 mm SL, Moorea, E. of pass out of Cook Bay on reef slope, 17°28.29′S, 149°49.17′W, 3.1–12.2 m, rotenone, field number RW89-29, R. Winterbottom, R. Holleman, and R. Mooi, 12 December 1989; ROM 60895, females, 13.9 and 14.9 mm SL, Moorea, N.E. tip of pass out of Cook Bay, 17°28.42′S, 149°49.22′W, 13.9–14.5 m, rotenone, field number RW89-37, R. Winterbottom and R. Mooi, 15 December 1989. OTHER MATERIAL EXAMINED: *Eviota randalli*- BPBM 9419 (2), 14.8–16.1 mm SL, males, Tahiti, Popote Bay, Papara, 9.2–12 m, chemfish, J.E. Randall, 13 March 1969; *Eviota pseudostigma*- CAS 43545 (2 paratypes, 15.0–19.2 mm SL), Amirantes Islands, J. Böhlke, R. Rosenblatt, et al., 2 March 1964; ROM 58949 (4, 11.1–15.1 mm SL), Comoros, Moheli, 12°23.52′S, 43°30.000′E, 2.0–5.0 m, rotenone, field number RW88-39, R. Winterbottom et al., 25 November 1988.

DIAGNOSIS.—The following combination of characters distinguishes *E. randalli* from congeners: dorsal-anal fin-ray formula 8/8; pectoral-fin rays branched, only starting with ray10 (usually 11 or 12); cephalic sensory-pore system pattern I (complete); fifth segmented pelvic-fin ray absent; three to four branches on fourth pelvic-fin ray, three to seven segments between branches (usually three or four); genital papilla non-fimbriate; dorsal fin slightly filamentous; three internal dark bars between anal-fin origin and caudal fin; a prominent dark spot on lower half of pectoral-fin base and a white area anterior to pectoral-fin base.

DESCRIPTION.—Dorsal-fin rays VI+I,8; anal-fin rays I,8; pectoral-fin rays 16 (16–18; 16.8), rays 11–13 branched (10–13); pelvic-fin rays I,4, fifth ray absent; branches on fourth pelvic-fin ray three (3–4), four (3–7) segments between branches; branched caudal-fin rays 11 (10–11); segmented caudal-fin rays 17 (17–19); lateral scale rows 24; transverse scale rows 7; breast scaleless; first dorsal fin of holotype not filamentous, slightly so in some specimens; pelvic fins reaching to genital papilla; cephalic sensory-pore system pattern I (complete); male genital papilla non-fimbriate.

Measurements: (based on holotype and eight paratypes): Standard length 16.8 (14.4–18.3); head length 29.8 (29.8–31.9; 30.8); origin of first dorsal fin 35.7 (32.5–38.9; 36.1); origin of second dorsal fin 55.6 (54.1–59.7; 56.8); origin of anal fin 58.9 (57.9–60.2; 58.9); caudal-peduncle length 24.4 (21.9–26.6; 24.4); caudal-peduncle depth 10.7 (9.1–11.6; 10.8); body depth 19.0 (18.0–21.4; 19.4); eye diameter 11.6 (11.1–12.1; 11.6); snout length 5.1 (4.1–6.5; 5.4); pectoral-fin length 34.8 (27.2–35.1; 34.8); pelvic-fin length 26.8 (26.8–37.4; 31.1).

Color in preservative: Background color of body, head, and fins straw colored. Sides and top of head with a peppering of small black dots extending onto the nape. A narrow broken line along top of head from behind eyes onto nape. A brown band extends anteriorly from anteroventral portion of eye across both jaws onto and across gular area. A second brown bar extends from posteroventral portion of eye across cheek half way to preopercle. Scattered small black dots on side of head concentrated on ventral half of preopercular margin forming a short bar. Space between this bar and pectoral-fin base immaculate until very dark brown band on lower half of pectoral-fin base. A scattering of dark dots above bar on upper part of pectoral-fin base. Sides of body with a pep-

FIGURE 1. Holotype of *Eviota randalli*, CAS 228572, 16.8 mm SL, female, Fiji, Cobia Island.

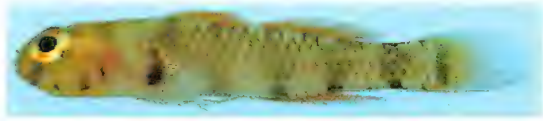

FIGURE 2. Paratype of *Eviota randalli*, ROM 60894, 16.8 mm SL, male, Moorea. Photo by R. Winterbottom.

pering of small dots and four complete internal dark bars, the anteriormost bar, anterior to anus and under pectoral fin; second bar just posterior to anal-fin origin; third bar just posterior to end of anal fin; fourth bar on caudal peduncle; ventral portions of bars two, three and four obvious dark brown to black spots. An incomplete dark bar present at dorsal-fin origin. Dorsal surface of body with dark brown spots along dorsal-fin bases corresponding to lateral internal bars on body. Scale pockets outlined by light brown pigment. Caudal-fin base with a light brown bar, remainder of fin with some fine peppering. Pectoral fin immaculate. Anal and dorsal fins with scattered light brown pigment on rays and membranes.

Color of fresh specimen: Pigment pattern in fresh specimen same as in preserved specimens except that internal lateral bars are black and more obvious. Background color of body white. Orange color on head: concentrated on snout, around anteroventral and posteroventral subocular dark brown bars and onto iris adjacent to bars; another orange blotch on top of iris, pupil black; preopercular area around black area on preopercular margin orange and more faintly onto cheek; posterodorsal area behind eye with an orange blotch; some scattered light orange pigment on nape. Band on ventral half of pectoral-fin base intense black, upper half of base above black band orange. Area anterior to pectoral-fin base white with no dark pigment spots. Dorsal ends of internal lateral bars under dorsal fins with orange. A slight orangish tinge on sides of body.

ETYMOLOGY.—The specific epithet is a patronym, a noun in the Latin genitive case, in honor of John E. Randall, who has greatly furthered *Eviota* systematics by photographing and collecting many species, including a number new to science.

COMPARISONS.—*Eviota randalli* has a complete cephalic sensory-canal pore configuration, belonging to Group I of Lachner and Karnella (1980). This group contained 22 described species (Shibukawa and Suzuki 2005, Matsuura and Senou 2006; and Allen et al. 2007), with the addition of *E. randalli* bringing the total to 23. *Eviota randalli* has a dorsal-anal formula of 8/8, whereas the following species in Group I have different formulas: 9/8 — *E. albolineata* Jewett and Lachner 1983, *E. disrupta* Karnella and Lachner 1981, *E. epiphanies* Jenkins 1903, *E. fasciola* Karnella and Lachner 1981, *E. guttata* Lachner and Karnella 1978, *E. inutilis* Whitley 1943, *E. irrasa* Karnella and Lachner 1981, *E. korechika* Shibukawa and Suzuki 2005, *E. melasma* Lachner and Karnella 1980, *E. natalis* Allen 2007, *E. readerae* Gill and Jewett 2004, *E. smaragdus* Jordan and Seale 1906; 8/7 — *E. pardalota* Lachner and Karnella 1978. 10/8–10/9 — *E. abax* (Jordan and Snyder 1901), *E. masudae* Matsuura and Senou 2006. The following described species in Group I share the dorsal-anal formula of 8/8 with *E. randalli*: *Eviota distigma* Jordan and Seale 1906, *E. herrei* Jordan and Seale 1906, *E. nebulosa* Smith 1958, *E. nigripinna* Lachner and Karnella 1980, *E. monostigma* Fourmanoir 1971, and *E. pseudostigma* Lachner and Karnella 1980. *Eviota randalli* has a dark mark on the pectoral-fin base whereas the base is light in *E. nebulosa*, *E. nigripinna*, and *E. herrei*. The fifth pelvic-fin ray is 10–20% the length of the fourth pelvic ray in *E. distigma* whereas it is rudimentary or absent in *E. randalli*, and it has prominent dark spots on the top of the head that are lacking in *E. randalli*. *Eviota monostigma* has the entire pectoral-fin base covered with a dark spot, whereas in *E. randalli* only the lower half of the base is intensely dark, and it has up to seven dark spots on the ventral midline from the anal-fin origin to the end of the caudal

peduncle whereas there are only three in *E. randalli*. *Eviota randalli* is most similar to *E. pseudostigma* (Fig. 3), the species it was previously called. The most obvious difference between the two is the coloration on the ventral surface, with *E. randalli* having three distinct dark spots between the anal-fin origin and the caudal-fin base that connect to internal bars, whereas *E. pseudostigma* has four (Fig. 3). There also are differences in the pectoral-fin rays between the two: *Eviota randalli* has 16–18 rays, whereas *E. pseudostigma* has 14–17 (Table 1); the greater difference is in the branching of the rays with the branching not beginning in *E. randalli* until the 10th to 12th ray, whereas branching can start with the third ray in *E. pseudostigma*. These differences that were first observed by Lachner and Karnella (1980) are supported by the additional Pacific Ocean material.

TABLE 1. Pectoral-fin ray counts for specimens of *Eviota randalli* and *E. pseudostigma*.

Pectoral-fin rays	14	15	16	17	18
Eviota randalli	–	–	8	8	4
Eviota pseudostigma	1	4	6	6	–

FIGURE 3. Holotype of *Eviota pseudostigma*, USNM 219289. Drawing from Lachner and Karnella (1980).

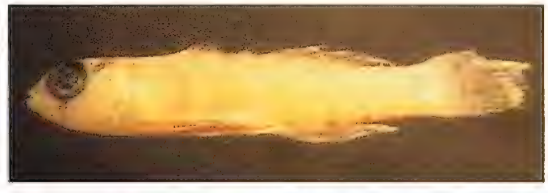

FIGURE 4. *Eviota* sp., ROM 84784, 11.3 mm SL, Palau.

Three small specimens of *Eviota* from Palau, ROM 84483 (10.1 mm SL), ROM 84766 (12.4 mm SL), ROM 84784 (11.3 mm SL), differ from other material examined. These specimens have four distinct dark spots on the ventral surface between the anal-fin origin and the caudal-fin base, similar to *E. pseudostigma*, but the branching of the pectoral-fin rays does not begin until at least the 10th ray as in *E. randalli*. In addition, the specimens have a bold, narrow bar extending down from the center of the eye to behind the maxilla that is absent in either species, and the pigmentation on the lower half of the pectoral-fin base is not as intense (Fig. 4). Until more, larger specimens are available these specimens will remain as *incertae sedis*.

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(New taxa are in **boldface** type)

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